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STUDIES ON THE HEAD IN FISHES

EMBRYOLOGICAL, MORPHOLOGICAL, AND PHYLOGENETICAL RESEARCHES

BY

NILS HOLMGREN

PART I:
DEVELOPMENT OF THE SKULL IN SHARKS AND RAYS.

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THE DEVELOPMENT OF DERMAL BONES IN THE SKULL OF AMIA CALVA

BY

TORSTEN PEHRSON

(With 50 figures in the text.)

INTRODUCTION.

In my paper on the cranial development of Teleostomian fishes (1922) I had the opportunity of showing that the dermal bones in Amia calva, related to sensory canals, develop in close connection to the sensory organs in the canals.

Further, I tried in the same paper to compare the rudiments of the canal bones in question with the canal bones in other recent fishes as well as in certain groups of extinct fishes, viz. Crossopterygians and Palaeoniscids in order to establish possible homologies between these bones.

As far as the origin of the canal bones is concerned my observations seem to be accepted (MOY—THOMAS 1938, 1939, WESTOLL 1937). Even the morphological value of the rudiments of the canal bones for comparative purposes has been accepted to a certain degree, especially by paleontologists, the objections advanced having chiefly concerned the interpretation of certain homologies (STENSIÖ, SÄVE—SÖDERBERG 1933, MOY—THOMAS, WESTOLL, PIVETEAU and others). Only ALDINGER (1937) denies emphatically the possibility of using embryological evidence for comparative morphological purposes.

Lately I have had the opportunity of examining a series of embryonic stages of Amia calva. This series is far more complete than the material on which I based my previous investigation. This new material was placed at my disposal by Professor NILS HOLMGREN, in whose institute, the Zootomical Institute of Stockholms Högskola, the investigation has been carried out. It is a great pleasure to me to express my gratitude to Professor HOLMGREN for his kindness and for his never-failing interest in my work.

This new investigation was made primarily in order to verify and complete my former work, chiefly by rendering it more convincing and clear in details by means of diagrams and reconstructions, secondly to make researches as to the development of some of the canal bones omitted earlier because of insufficient number of embryonic stages, and thirdly to try to throw some light on the origin of the dermal ossifications of the skull not connected with sensory canals.

My intention was also to use the morphological results of the embryological researches for comparisons with the dermal skeleton of the head of Crossopterygians and Actinopterygians, as our knowledge of fossil fishes has been considerably enlarged during the last decade.

The investigation has been carried out on the following embryonic stages (body length measured after fixation):

Amia calva: mms 7.5, 8.0, 9.0, 9.5, 9.9, 10.0, 10.4, 11.5, 12.0, 12.5, 13.2, 13.8, 15.7, 16.1, 16.5, 17.0, 18.2, 19.5, 20.0, 21.5, 22.0, 31.5, 34.5, 45.0, 56.0. The specimens are in complete series of transverse sections, thickness 6—8 μ, only the largest specimens in thickness 15 μ.

A. FORMATION OF CANAL BONES.

General observations.

In the paper already referred to (PEHRSON 1922) an account has been given concerning the development of canal bones in Amia calva from the point in their ontogeny, when osseous tissue is already beginning to form. One object of the present investigation has been to trace the origin of the osteoblasts, later to form the canal bones. To that end a thorough examination has been carried out of earlier embryonic stages than those hitherto investigated by the author.

In early stages of the formation of the sensory canals, where the canal organs themselves are still situated on a level with the surface of the epidermis, or, as far as the frontal parts of the head are concerned, in shallow grooves, the epithelium of the future canal is differentiated from the rest of the epidermis by its height. Under the epithelium is a very well defined basal membrane. In these early stages however the basal membrane underneath the canal organs (neuromasts) and chiefly under their caudal part is broken, partly dissolved, and often quite invisible. The same condition is shown as well under the parts of the future canal, situated in the immediate vicinity of the canal organs.

The mesenchyma is generally rather sparsely nucleated. But in the places where the basal membrane is broken up a densely nucleated mass is formed, where there is no possibility of distinguishing epithelial nuclei from mesen-

chymateous cells. The same phenomenon is to be seen in all parts of the lateral line system of the head, in stages before the formation of the canal bones, and always in connection with the canal organs. Under the basal membrane in the course of the future canal, and on both sides of the sense organs—rostrad and caudad where the canal runs in caudo-rostral direction—a thin stratum of nuclei is formed. Where the sense organs are situated close to each other, and develop fairly simultaneously, this thin nucleated area forms a sort of tape-like layer under the future canal, connecting the densely nucleated masses under the sense organs with each other.

What suggests itself is certainly a proliferation of cells from the canal organs and their close vicinity in the epithelium. The proliferation seems to be accompanied by a migration of cells into the underlying mesenchyma, where they spread along the course of the future canal.

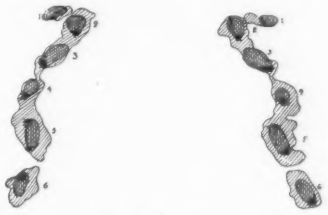

Fig. 1. Amia calva, 10.4 mm. Dorsal view of the supraorbital line. (42 × 1.) *1—6*, supraorbital sense organs. Vertical lines, sense organs; oblique lines, osteoblastic lining; short horizontal lines, places of migration of cells.

In fig. 1 is seen a reconstruction of the supraorbital canal including the supraorbital sense organs 1—6 in the 10.4 mm stage. The reconstruction shows the elongated nucleated area that closely follows the track of the canal. Organ 6, which is slightly later in developing, has its own area of cells. To the left, between organs 3 and 4, a deep indentation on both sides of the area indicates recent fusion of the nucleated strata originally belonging to, and formed by the two organs in question. The same condition is seen to the right between organs 3 and 4, as well as between organs 4 and 5 to the left. Fig. 2 is a profile reconstruction showing the supraorbital and the first part of the infraorbital canal at the same stage (10.4 mm). The situation of the rostral canal, immediately dorsally to the rostral end of the larval sucking apparatus, makes exact observations of cellular proliferation from the four rostral sense organs difficult, especially as in cross sections, the only sections made, the canal is cut lengthwise. To a certain degree the same reservation applies to the first organ in the supraorbital line. From the third organ in the infraorbital line (the two rostral organs on each side being numbered 1 and 2) the condition is very much the same as described in the supraorbital line. The basal membrane, mostly very sharp and well defined, is broken up and blurred in one or two places under the canal organs, resp. the adjacent parts of the epithelium. Congregations of nuclei there protrude into the mesenchyma. Further there is a thin lining of nuclei immediately under the part of the epithelium, where the canal will eventually form. The lining begins slightly rostrally to canal organ 2, follows the course of the canal, and ends in this stage behind organ 7. Just as the

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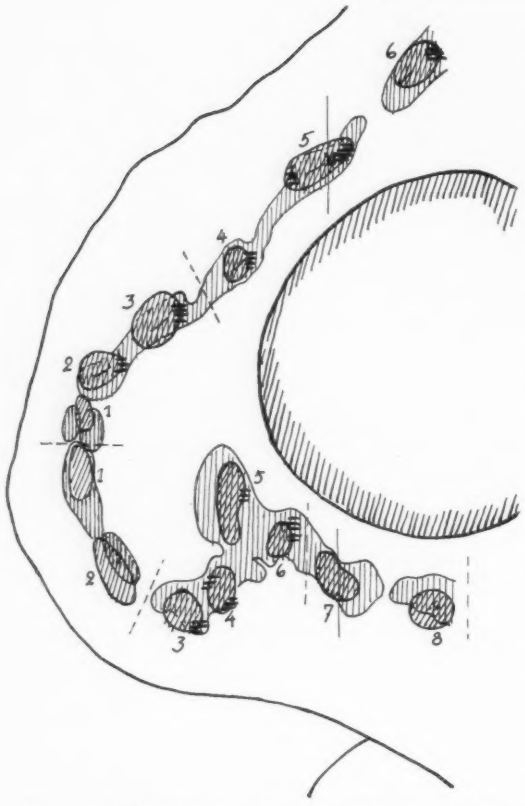

Fig. 2. Amia calva, 10.4 mm. Lateral view of the head with supraorbital line and beginning of infraorbital line. (84 × 1.) *1—6* (dorsal), supraorbital sense organs; *1—8* (ventral), infraorbital sense organs. Oblique lines, sense organs; vertical lines, osteoblastic lining; short horizontal lines, places of migration of cells; broken lines, boundaries between future bones; long vertical line through s.o. organ *5* and i.o. organ *7* denotes position of cross-section in microphotographs fig: s 3 and 11 resp.

nuclear lining in the supraorbital line includes the organs that are later to belong to the nasal bone and the rostral part of the frontal, thus making a gap between the second and the third organ in the future frontal bone, the nuclear stratum in the infraorbital line has a gap between the two organs which are later to belong to the lacrymal bone. Between organs 4 and 5 in the infraorbital line there is a deep incision on each side.

An interesting fact is, that the cellular proliferations forming under the organs in the supraorbital line appear to be markedly bilateral. No such tendency can be traced in the corresponding places in the infraorbital line. As shown earlier (PEHRSON 1922) the bones form as binary rudiments in the supraorbital line but as single elements in the infraorbital.

The observations now indicated and their interpretation seem to tally with KLAATSCH's theory on the origin of scleroblasts in Salmo (KLAATSCH 1894). In my earlier paper (1922) I denied having seen anything that could be interpreted as migration of scleroblasts from the ectoderm, a mistake probably due to lack of material of sufficiently early stages of bone formation. The recent observations might be interpreted as migration of cells from the ectoderm and the ensuing spreading of the cells under the future canal. In stages slightly older than the ones described above, the gaps in the nuclear stratum are filled up, thus indicating a wandering of cells from the place of their formation, i.e. migration.

The microphotograph shown in fig. 3 agrees very well with KLAATSCH's drawings of the stages he has described as migration of cells from the precise

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parts of the epithelium, where I have found the corresponding conditions. SCHLEIP (1904), who has tested KLAATSCH's theory on Salmo, thus KLAATSCH's own material, could not find any signs of an ectodermal origin of the scleroblasts. Without expressing any opinion as to whether there is a migration or not or whether or not there are scleroblasts formed from the ectoderm in Salmo, I want to mention that I have found the same conditions as in Amia in a six weeks old fry of Salmo salar, viz. the breaking up of the basal membrane under the canal organs and a mass of nuclei protruding into the mesenchyma.

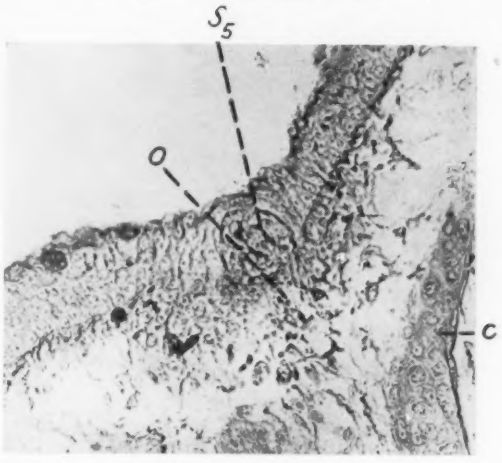

Fig. 3. Amia calva, 10.4 mm. Cross-section of supraorbital sense organ 5. S_5, sense organ; *o*, migrating osteoblasts, *c*, cartilage. Microphotograph.

The processes now described take place rather early in the anterior part of the canal system. Further back in the head of Amia the same conditions are found, only later. Thus the forming of osteoblasts from the organs in the supratemporal commissure or the anterior part of the main sensory canal of the body takes place at a stage when the bones in the anterior part of the head are already fairly well developed.

In the next stage of the formation of bones there are clusters of nuclei, found in the places where subsequent ossification will take place. The conditions found in a 11.5 mm stage in the same parts of the infraorbital canal as have been referred to above are pictured in the microphotograph fig. 4 and the reconstruction fig. 5. There are two clusters of nuclei visible. One is

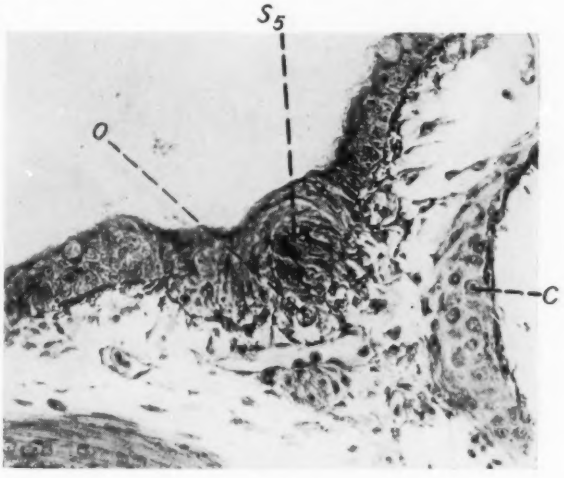

Fig. 4. Amia calva, 11.5 mm. Cross-section of supraorbital sense organ 5. Letters as in fig. 3. Microphotograph.

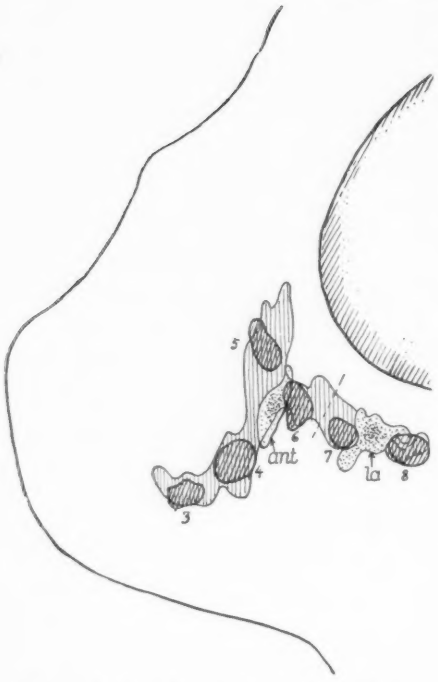

Fig. 5. Amia calva, 11.5 mm. Lateral view of snout with infraorbital sense organs 3—8. (84 × 1.) *ant*, antorbital primordium; *la*, lacrimal primordium; oblique lines, sense organs; vertical lines, osteoblastic lining; dotted, blastema.

connected with the sense organs 4, 5 and 6, although situated nearer to and underneath the anterior part of organ 6. The second cluster lies between, and partly under, organs 7 and 8. Unlike the masses of nuclei seen in the previous stage, where they were situated immediately under the epithelium, these clusters are separated from it by a thin layer of sparsely nucleated mesenchyma. Yet the former area of nuclei under the epithelium between the sense organs is still present, and so are the broken-up parts of the basal membrane. The two clusters are not sharply delimited from the surrounding mesenchyma. In the adjacent parts of the mesenchyma there are to be seen numerous elongated nuclei. They connect the clusters with the nucleated lining under the basal membrane. That lining now connects the infraorbital sense organs 7 and 8 as well, where there was a gap in the 10.4 mm stage.

The conditions now described may be interpreted in the following way. From the sense organs and their immediate neighbourhood a migration of cells takes place. The cells spread under the epithelium where the sensory canal will subsequently develop. Where there are closely situated sense organs, and the migration process takes place almost simultaneously, a real path of cells is formed, but in other cases there arise defined areas that may fuse later. The migrating cells are osteoblasts or will later develop into such cells.

The osteoblasts wander through the mesenchyma, and gather to take part in the formation of the blastema of the future ossification. In the case now described, there are formed two blastemas, the anterior developing into the antorbital bone, the posterior into the lacrimal.

In a 12 mm specimen these two bones are already formed (fig. 6). The migration of cells has ceased, for the basal membrane shows no signs of being broken up. Further, there are scarcely any cells visible under the basal membrane between the sense organs. According to the interpretation given above, all the osteoblasts have moved away to join the blastemas. In the

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case of the primordium of the antorbital there are now practically no cells underneath the sense organs themselves, as the whole body of osteoblasts is concentrated in the young bone. The growth of the bone is indicated by osteoblasts around its edges. The result is seen in the reconstruction showing the conditions in 13.8 and 16.1 mm specimens (fig. 13 and 14). The description of the development of the antorbital is applicable to the histogenesis of any bones related to sensory canals, differences only arising in respect to morphological points of view. As will be shown later, one bone may develop in connection with only one sense organ, or from two organs, etc.

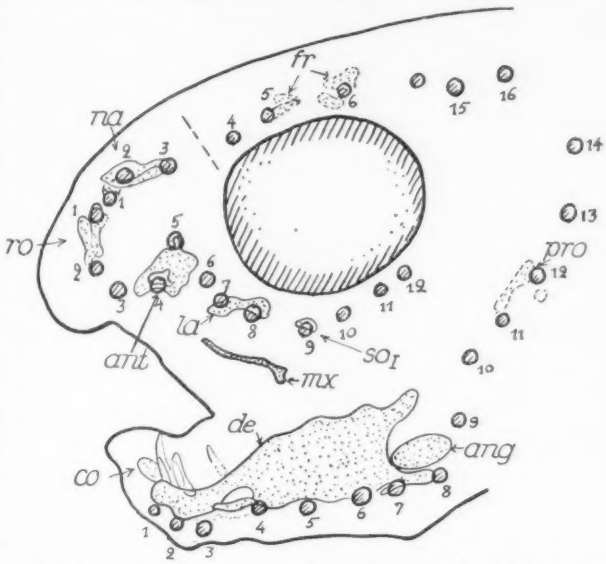

Fig. 6. Amia calva, 12 mm. Lateral view of head with sense organs and bone primordia. (42 × 1.) Dotted surrounded by unbroken outline, bone; dotted surrounded by broken outline, blastema. For letters, see key, pages 47—48.

The formation of the dermal ossifications which arise in connection with the sensory canals seems to take place in two, or rather three, different stages. The first process is the formation of the osteoblasts, and their migration under the epidermis. The result of this process is the formation of primary blastemas under each separate sense organ, and of a stratum of osteoblasts under the future canal. The primary blastemas may have a certain morphological value, as the ones formed in connection with the infraorbital line are single, whereas the primordia belonging to the supraorbital line seem to be more or less markedly bilateral. As known (PEHRSON 1922) the bones in the supraorbital line arise from double rudiments, while the infraorbital ossifications are single from the beginning. Possibly the primary rudiments represent an earlier phylogenetic condition, when protecting scales were formed in connection with each separate sense organ. The value of this surmise will be dealt with later.

The next stage is the formation of the blastemas which are to give rise to the ossifications. They arise as a result of the gathering in the mesenchyma of the previously formed osteoblasts. These secondary blastemas may or may not arise in connection with each separate sense organ. Therefore, in the part of the infraorbital canal occupied by the sense organs 3—8

two blastemas are formed, later to develop into the antorbital bone and the lacrimal bone respectively. As will be shown later in the description of the development of each separate bone, blastemas, and even ossifications may arise under each single sense organ, the future bone thus being formed as a result of the joining of different units. This is the case, for instance, with the supratemporo-intertemporal bone. In other cases again the development will be the result of both processes.

Bones developing in connection with the supraorbital canal.

Nasal. The first development of this bone has already been described above. As to the later stages of development the observations referred to in my earlier paper (1922) may be confirmed as far as the general description goes. As to details, a reservation seems necessary concerning the development of independent binary rudiments under the canal organ 3. Secondary blastemas form plainly in connection with organs 1 and 2, as is shown in fig. 7 representing a reconstruction from a 12 mm specimen. The binary rudiments are already ossified, although still remaining individual, at least on the left side. On the right side the rudiments under organ 2 have begun to fuse. No well outlined blastemas, or bone rudiments, seem to form under organ 3. Instead the rudiments under organ 2 develop very quickly, the result being a single bone gutter that rapidly joins and overtakes the indistinct blastema aggregation under organ 3. The result is seen in the reconstruction from a 13.2 mm specimen (fig. 8) where the binary tips of the bone are growing under organ 3 and caudad.

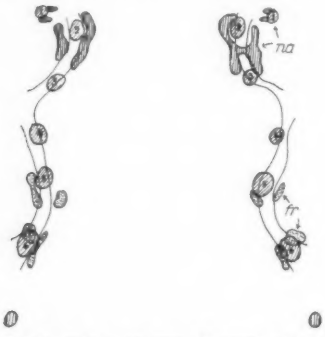

Fig. 7. Amia calva, 12 mm. Dorsal view of supraorbital canal, showing primordia of nasals and frontals. (42×1.) Oblique lines, sense organs; vertical lines, bone; dotted, blastema. Circle behind organs 6, first organ in anterior head line of pits.

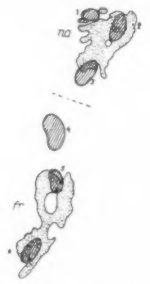

Fig. 8. Amia calva, 13.2 mm. Dorsal view of left nasal and frontal. (42×1.) For letters, see key, pages 47—48.

The morphological significance of the composite origin of the nasal, as well as of other canal bones, will be discussed later.

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Frontal. The primary origin of this bone in a 10.4 mm specimen is shown in fig. 1. In a 12 mm specimen there are formed binary, secondary rudiments, though not yet ossified under the organs 5 and 6 (fig. 7). Contrary to my earlier suggestion (1922) and as a result of examining a more extensive series of embryos, I have found that probably there are no separate rudiments forming under organ 4. The binary rudiments seen in a 12 mm specimen under organs 5 and 6 fuse first with their respective vis-a-vis. Thus a single gutter-shaped unit is formed under the two organs. The two rudiments then fuse, chiefly because of the rapid growth of the bone under organ 6, as seen in a 13.2 mm specimen (fig. 8). The bone now grows at both ends, thus extending even under organ 4 as shown in a 17 mm specimen (fig. 9), where the two tips of the left frontal already have grown slightly under organ 4. The right bone is a little slower in developing.

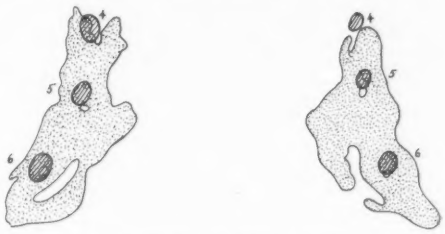

Fig. 9. Amia calva, 17 mm. Frontals, dorsal view. (40×1.) *4—6*, supraorbital sense organs.

From the caudal end of each frontal a single tongue will grow backward to extend eventually under organ 7. This organ seems to be unable to form any osteoblasts. In this respect it resembles the rest of so-called pit line organs. Considering the great importance pit lines play in the paleontological literature as supposed morphogenetic elements, it is a remarkable fact that no proliferation of nuclei seems to take place from them. In Amia, at least, they seem unable to take any active part in the formation of bones.

Bones developing in connection with the infraorbital canal.

Rostral (ethmoid). In my earlier description of the development of the rostral in Amia (1922) I stated that this bone is formed from four, possibly five, distinct components. The four elements are formed in connection with the four sense organs in the ethmoidal commissure, whereas the fifth possible unit was supposed to be a median rudiment. The new investigation has shown that there is no such element. The origin of the rostral is shown in fig. 10 representing a reconstruction of the sense organs in the snout of a 12 mm specimen, seen from above. The two first sense organs on each side in the infraorbital series are to be seen. In connection with each one is a separate, blastematic primordium in the second stage of development, in accordance with the scheme indicated in the

Fig. 10. Amia calva, 12 mm. Dorsal view of sense organs and bone primordia in rostral commissure. (62.5 × 1.) Vertical lines, sense organs; dotted, blastema.

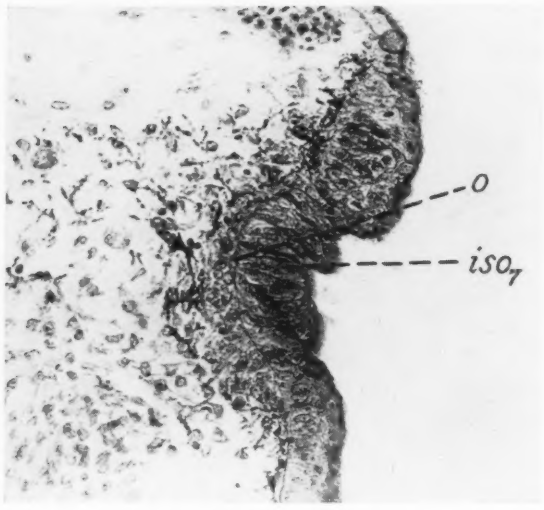

Fig. 11. Amia calva, 10.4 mm. Cross-section of infraorbital sense organ 7. iso_7, sense organ; *o*, osteoblasts. Microphotograph.

general part of this account. The four rudiments fuse later, but comparatively early, to form one cylindrical bone.

Antorbital and *lacrimal.* The earliest phases in the development of these two bones are described above.

The antorbital forms in connection with the sense organs 3—6 in the infraorbital line. Like the rest of the bones in this line, including the rostral, the antorbital does not develop from binary rudiments (cfr. figs. 11 and 12), a peculiarity they share only with the bones in the supra-temporal commissure. Another peculiarity of the antorbital is that although connected with not less than four sense organs it does not originate from a series of rudiments. After the migration phase in the development the osteoblasts collect in one spot, as mentioned above. In spite of careful investigation it has been impossible to discover any indication of a serial arrangement of rudiments, except during the primary phase of the development. In a 11.5 mm specimen a blastema has formed chiefly in connection with organs 4 and 6, as already mentioned (fig. 5). Ossification begins to take place at this stage. In a 12 mm specimen (fig. 6) an irregular bony shield has formed, spreading as a result of growth round the edges. The shape of the bone in a 13.8 mm specimen is shown in fig. 13 and in a 16.1 mm stage in fig. 14.

According to WESTOLL (1937 d) organs 3 and 4 should be interpreted as belonging to the rostral commissure, while 5 and 6 represent the beginning of the infraorbital canal dragged upwards. If this opinion is correct, the sense organs in the rostral commissure would form the four separate rudiments of the rostral (see above) and then contribute to the formation of the anterior half of the antorbital, while the posterior half would be formed from the first organs in the true infraorbital canal. This would not have been improbable if the antorbital had originated from separate primordia. The supratemporo-intertemporal, for instance, is formed in connection with three different sense organs, which receive their nerves from two different sources, but then the bone is to be considered as a complex bone, arising from

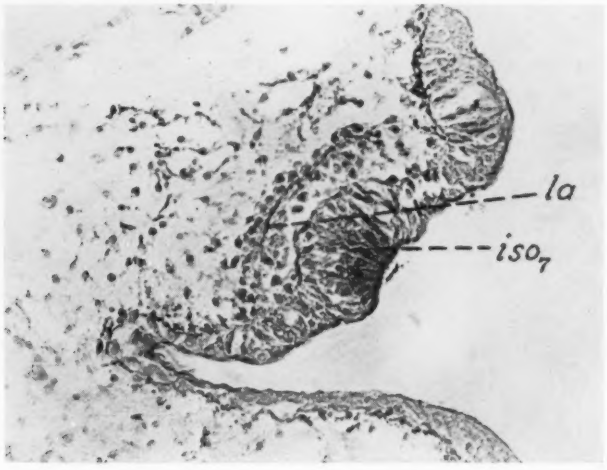

Fig. 12. Amia calva, 12 mm. Cross-section of infraorbital sense organ 7 and primordium of lacrimal. *la*, lacrimal primordium; *iso7*, sense organ. Microphotograph.

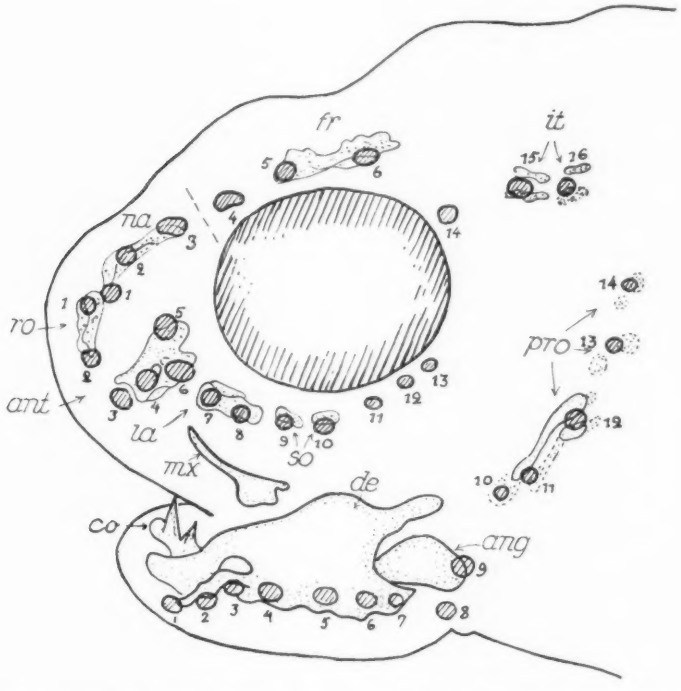

Fig. 13. Amia calva, 13.8 mm. Lateral view of head with sense organs and bone primordia. (42 × 1.) Dotted outlines, blastema. For letters, see key, pages 47—48.

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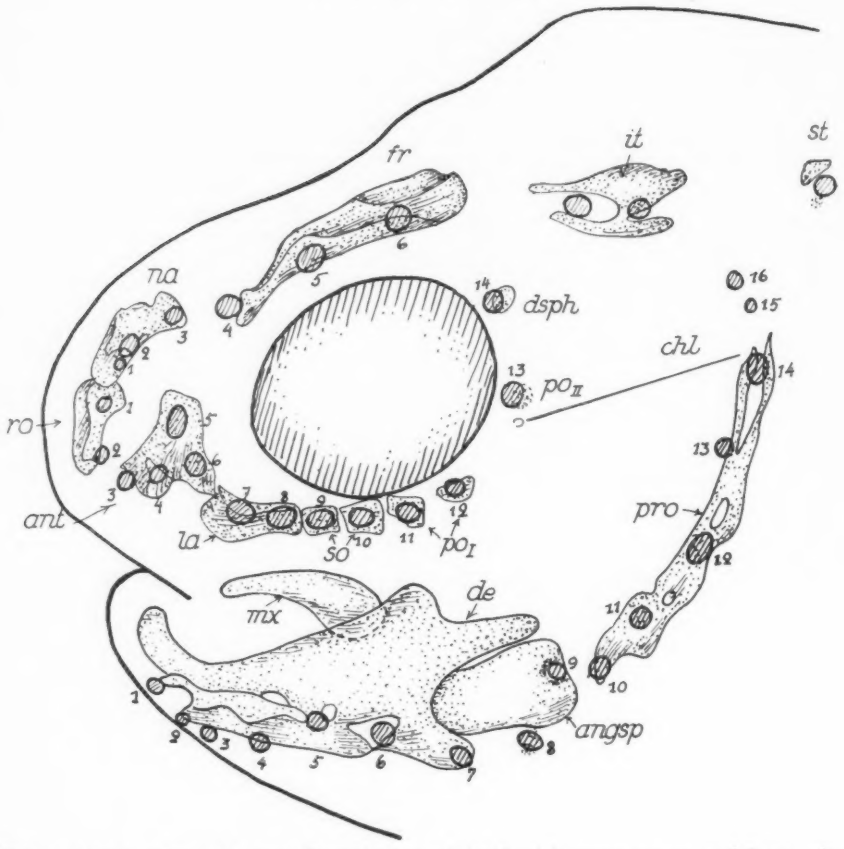

Fig. 14. Amia calva, 16.1 mm. Lateral view of head with sense organs and bone primordia. (42 × 1.) For letters, see key, pages 47—48.

different, separately formed units. As is shown above this is not the case as far as the antorbital is concerned. On the contrary, this bone develops as one unit. Hence it seems reasonable to believe that the sense organs, connected with it morphologically, belong to the same part of the canal system.

The lacrimal forms in connection with the infraorbital organs 7 and 8. During the migration phase the area of osteoblasts under no. 7 is connected with the nuclear lining under the anterior part of the infraorbital line, whereas a separate cluster of cells is situated under organ 8 (fig. 2). Later on the anterior and the posterior areas fuse, and one single blastema is formed as seen in the 11.5 mm specimen and fig. 5 (cfr. figs. 11 and 12). The bone then grows in the usual way, forming first a gutter, then a cylindrical piece.

Sub-(infra-)orbitals, postorbitals and *dermosphenotic.* The development of bones related to the posterior part of the canal takes place later than in the

anterior part. In the 12 mm specimen a bone rudiment is found under organ 9, and in the 13.8 mm specimen one under organ 10 (figs. 6 and 13). They are the two suborbitals.

In the 16.1 mm stage (fig. 14) another bone has developed under organ 11, and one more under organ 12. In connection with organ 13 there is in this stage still only a blastema formed, whereas a small round bony disc is to be seen under organ 14. This is the primordium of the dermosphenotic. While this bone as well as the one under organ 14 (postorbital II) grows in the normal way to form separate bones, the bone rudiments related to organs 12 and 13 take a slightly different course. In my former paper (1922) I was not able to describe the development of postorbital I with certainty, owing to a gap in the material. As is seen from the description above, bone develops comparatively late in connection with organ 13. As the bone in an adult Amia contains organs 12 and 13 it might be supposed that ossification takes place by means of the enlarging of the bone under organ 12. That is, however, not the case. In the 20 mm specimen a bone disc has formed under organ 13 and in the 22 mm specimen it has changed into gutter shape, and grows in rostro-ventral direction towards the bone connected with organ 12. For quite a long time the two bones develop separately but in the 56 mm specimen, the oldest I have had at my disposal, the two bones have fused into one single piece. In the 45 mm specimen the two elements are still independent.

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Thus in the infraorbital line two different principles of development of bones connected with more than one sense organ are exhibited. The antorbital and the lacrimal form, from the beginning, one separate unit each. These units develop in toto by means of growth round the edges into the respective bones, the antorbital including four and the lacrimal two sense organs. The postorbital I, on the contrary, arises as two distinct units, which remain separate for a comparatively long time, later to fuse into one composite bone.

The development of the rostral follows a slightly different course. The bone has its origin from four distinc units, but they fuse at a very early stage to form one bone. From phylogenetic point of view it may perhaps indicate that the change of four free rostrals into one single bone is probably a very old process, whereas the development of the duplicate postorbital I is to be considered as a comparatively late process.

Another modification in the development of bones with more than one sense organ is found in the supraorbital line. Here too separate rudiments fuse very early as compared with the corresponding process in the postorbital I. Individual bone rudiments are not formed under each separate sense organ. To a certian degree they develop therefore in the way described above concerning the antorbital and the lacrimal.

The various ways of development of the bones in the supra- and the infraorbital lines seem to justify the principle suggested by WESTOLL (1936), applied by FORSTER—COOPER (1937) and later adopted by MOY—THOMAS (1938 a) of using the notion of "series" when naming the different ossifications arising in connection with the sensory lines. The method seems useful as a provisional way of naming bones without expressing any opinion on their homologons in other fishes, and thus without penetrating deeper into the genetical problems. Much ink might have been saved and many mistakes avoided if a preliminary enumeration of the ossifications in different "series" had been made in descriptions of fossil forms especially. A gradation along genetic lines might then have been postponed till sufficient material had been collected. A simple naming of the bones with letters or figures does not imply an attempt at homologizing bones, as is the case when names such as antorbital or lacrimal are used.

Supratemporo-intertemporal. This bone arises in connection with the infraorbital sense organs 15 and 16, and, as well, with no. 1 in the main lateral line.

Fig. 15. Amia calva, 17 mm. Lateral view of left intertemporal. (42 × 1.) *15, 16,* infraorbital sense organs.

In my former description of the origin of the bone (1922) the intertemporal part was supposed to form in one single piece from organ 15. This is a mistake, however, due to insufficient material. As a matter of fact the bone is formed from three separate binary rudiments. In a 13.8 specimen (fig. 13) binary rudiments are formed in connection with canal organs 15 and 16. Three of the rudiments are already ossified. Only the lateral one belonging to organ 16 still remains in the blastema stage. In a 17 mm specimen the four rudiments have fused to form an H-like piece of bone (fig. 15). This is the intertemporal part of the supratemporo-intertemporal.

As to the supratemporal part, it appears as a binary rudiment in the 16.1 mm specimen, and connected with the first sense organ in the main lateral line (fig. 14). Even here the medial rudiment is already ossified, the lateral one still remaining in the blastema stage. In this specimen a horizontal lamella is already forming from the medial part of the intertemporal component of the bone.

Seemingly there is a slight discrepancy in the development of the bone in different specimens, as it is further advanced in a 16.1 mm specimen than in a 17 mm one. Such apparent variations may be due to different causes. One is that the measurements of different specimens selected for examination are never quite to be relied upon, owing to the conditions of the embryos. Further the process of development always varies slightly in different specimens. A real gradation of the material could only be made by determining the degree of development of a special organ, for instance some special bone. But there again we meet with the difficulty that different organs

do not always develop with the same rapidity. Thus not too much stress should be laid upon the figures indicating the length of the embryos. They refer simply to the actual conditions found in each case. Therefore a 12 mm specimen examined in my former investigation, does not necessarily tally with an embryo of the same length examined now.

There seems to be no doubt that the intertemporal and supratemporal parts of the developing composite bone correspond to the similarly named bones in Osteolepidae and Rhizodontidae. The congruence is ascertained by the fact that in Osteolepis (SÄVE—SÖDERBERG, 1933, pl. 4) and in Macropoma (STENSIÖ, 1937) the intertemporal may sometimes be subdivided in two independent bones, corresponding to the two separate rudiments in the embryo of Amia.

Parietal. This bone is not directly connected with the sensory canal system. On the other hand it is, at least topographically, related to pit lines. The system of pit lines is generally considered to be morphologically related to the sensory canal system in fishes. In all modern palaeontological works on fishes it plays an important part as an auxiliary means for the establishing of homologies. The morphological value of the pit lines seems often to be considered equally important as that of the canal system.

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As soon as it was discovered in this investigation that the cellular material of the canal bones had its origin in the canal organ themselves, and their immediate vicinity, the question arose whether the pit line organs were of similar importance to the bones related topographically to them. In Amia there are two bones of that kind, the parietal and the gular bones. The parietal carries the anterior, middle and posterior head lines of pits. Across the gular runs the gular line.

As has already been pointed out in this paper (page 9) I have not been able to discover any signs of proliferation of cells from pit organs. The development of these bones has been examined, however. A description of the origin of the parietal will be given below, whereas the development of the gular is dealt with in page 47.

The first indication of the parietal can be observed in a 16.5 mm specimen as a thin layer of osteoblasts in the mesenchyma on each side of the head over the brain. It is situated on a level with the supraorbital organ 16 (thus the caudal of the two intertemporal sense organs). The intertemporal rudiment in this stage is still not fused with the supratemporal element. The small parietal rudiments are connected with the caudal part of the intertemporal rudiments by means of an area, more sparsely nucleated than the parietal rudiment itself but yet contrasting with the mesenchyma with its still rarer nuclei. In this stage the intertemporal has already developed a thin ossified median lamella (cfr. fig. 14). The inner edge of this lamella is not sharply

defined against the thin layer of nuclei that connects it with the parietal rudiment.

In a 18.2 mm specimen the parietal rudiment has increased chiefly rostrad but is not yet ossified. The intertemporal and supratemporal rudiments have now fused. Irregular streaks of sparse nuclei connect the median lamella of the bone with the parietal rudiment. It is not possible to make a trustworthy graphic reconstruction because of the difficulty of defining the blurred outlines of the very thin layer of osteoblasts.

In a 20 mm specimen ossification has begun. As is shown in fig. 16, the parietal rudiment on each side consists of two different pieces, one larger rostral and one smaller caudal. Whereas the rostral rudiment chiefly consists of bone, in various places bordered by areas of not yet ossified tissue, the caudal part is formed of a couple of ossifications surrounded by osteoblasts The two parts are separated by a gap, where there is only ordinary mesenchyma. But, as is the case in the earliest stages, there are still streaks of tissue more densely nucleated than the surrounding mesenchyma, and connecting the parietal rudiments with the supratemporo-intertemporal rudiment. While it is easy to define the parietal rudiments at this stage from the mesenchyma, even where no ossification has so far taken place, the outlines of the connecting streaks are rather difficult to outline as there is every degree of nucleation from the conditions in the rest of the mesenchyma to a comparatively easily discernable tissue. Fig. 16 will give a fairly good idea of the conditions. As seen, even the nucleated streaks are divided into one rostral and one caudal part on each side, each one corresponding rather well to the subdivision of the parietal rudiments. In the reconstruction, the irregular, uneven, median edges of the supratemporo-intertemporal rudiment should be noted.

In a slightly older specimen, measuring 22 mm, the parietal rudiments on each side have fused, the ossified part so far only on one side, and the whole rudiment has grown chiefly caudad (fig. 17). The subdivision of the streaks connecting the parietals with the supratemporo-intertemporals is still visible. The next stage at my disposal, a 31.5 mm specimen, shows the conditions of the adult.

The interpretation of the development of the parietals is as follows. The parietals are forming in close connection with the supratemporo-intertemporals. From the intertemporal and the supratemporal primordia, respectively, osteoblasts migrate towards the midline of the head. On each side they form a thin lamella of osteoblasts in the mesenchyma. This lamella develops into the parietal rudiment. As there is, originally, one rudiment formed as a supratemporal product and one derived from an independent intertemporal element, two parietals are formed on each side. That the intertemporal parietal rudiment in its turn should be split up in two, as the intertemporal

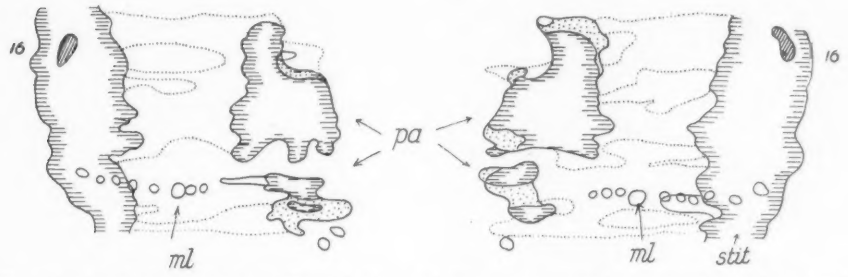

Fig. 16. Amia calva, 20 mm. Dorsal view of supratemporo-intertemporals and parietal primordia. (42 × 1.) Oblique lines, sense organs; white circles, pit line organs; horizontal lines, bone; dotted, blastema; dotted outline, blastematic connection between supratemporo-intertemporals and parietal primordia. *16*, infraorbital organ 16.

itself has formed from two elements, is an assumption that does not seem unreasonable, though I have not been able to prove it.

If this theory is correct, it may probably throw new light on the "squamosal" problem in fishes. In the "squamosal" complex should be included the parietals as well, as elements similar to the intertemporal and supratemporal bones.

In Amia the two pairs of parietals fuse to form one parietal on each side. On the other hand two pairs of parietals are known to have existed in various fossil fishes (Eusthenopteron, SÄVE—SÖDERBERGH, 1937; Acentrophorus, GILL, 1923; Saurichthys, STENSIÖ, 1925).

The parietal, supratemporal and intertemporal elements were free in the Rhipidistia and early Actinopterygians, as for instance Cheirolepis. The

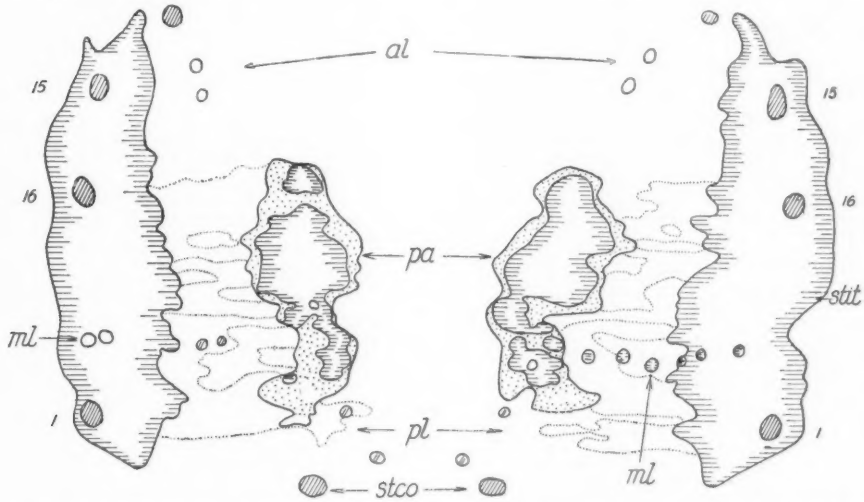

Fig. 17. Amia calva, 22 mm. Dorsal view of supratemporo-intertemporals and parietal primordia. (42 × 1.) *1*, first sense organ in main body line. Other denotations as in fig. 16.

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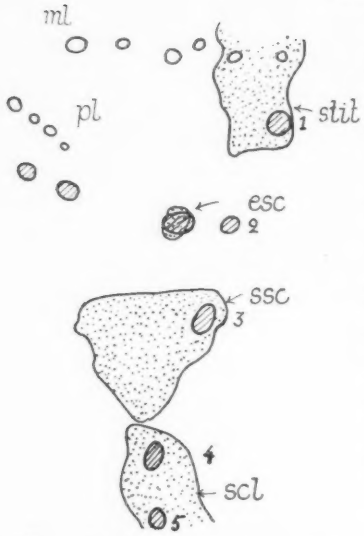

Fig. 18. Amia calva, 21.5 mm. Dorsal view of right supratemporo-intertemporal, extrascapular primordium, suprascapular and supracleithral. (42×1.) *1—5*, first five sense organs in main body line; white circles, pit organs; dotted, bone.

Coelacanthini possessed a parieto-intertemporal, Macropoma, for instance, a parieto-supratemporal, and in Polypterus all three elements are fused to form a parieto-supratemporo-intertemporal, while Amia, like most Actinopterygians, has free parietals and supratemporo-intertemporals.

Extrascapular. In my earlier investigation I had not the opportunity of examining in detail the development of this bone, for it develops rather late, and I had not a sufficient number of embryonic stages at my disposal. From the specimens examined now I am able to give at least a more detailed account, even if there are still some stages lacking. The result tallies fairly well with my earlier surmises.

In adult specimens the supra-temporal commissure contains three sense organs on each side of the median line and connects the main lateral line on each side, with beginning (and ending) in sense organ 2. Including these organs there should thus be eight organs altogether in the commissure. In early stages there are only two organs to be seen (the lateral organs excluded). The full number of sense organs is reached by the division of the most lateral organ on each side (the one situated immediately medial to the lateral line organ). The division takes place in the 17 mm to 21 mm specimens, though somewhat irregularly. In the 21.5 mm specimen shown in fig. 18, the division of the left organ is not entirely completed.

The first bone rudiment is found under the most lateral of the commissure organs, not under the lateral line organ. This is shown in fig. 18. In the next stage a separate bone rudiment is formed under the most medially situated organ (22 mm specimen, fig. 19). But in that specimen there is an aggregation of osteoblasts, indicating formation of one more rudiment, even under the interlying organ. It is situated in close connection with the first mentioned bone rudiment. I have not at my disposal any stage between these two, but, judging from the conditions on the left side in the 22 mm specimen, I am inclined to believe that a separate blastema has formed under each of the three organs of the commissure. If that is the case with the lateral line

Fig. 19. Amia calva, 22 mm. Dorsal view of extrascapular primordium (right half). (42 × 1.) *2*, second sense organ in main body line; oblique lines, sense organs; horizontal lines, bone; dotted, blastema.

organ, it cannot be discovered in my material as the rudiments have fused in my next stage (31.5 mm) and a single bone is formed, including even the main line organ. The rudiments, even in the blastema stage are single, not binary.

Without any doubt the extrascapular in Amia is formed by at least four different rudiments. It is even probable there are six rudiments taking part in formation of the bone. Whether there are eight or only six is, unfortunately, impossible to determine at the present stage. The presence of eight rudiments would agree with the number of extrascapulars found in Sinamia (STENSIÖ, 1935).

Suprascapular and *supracleithral.* The suprascapular is formed by a single rudiment in connection with the main line organ 3, and is first visible in a 21.5 mm specimen (fig. 18). The supracleithral develops comparatively early in connection with the main line organs 4 and 5. In a 13.8 mm specimen there is still no sign of the bone, but in the nearest stage at my disposal, a 15.7 mm specimen, it is already fairly well developed and bears a good sized lamella (cfr. fig. 18).

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Bones developing in connection with the preoperculo-mandibular line.

Two different morphological bone units develop in relation to the mandibular part of the sensory canal system of the head. They are the splenial elements belonging to the dentary and to the angular. The dentary, or dental, as it should be called here (in order not to cause confusion, the dental being one single unit) and the angular, however, have a different origin, as will be shown later in this paper, and develop without any connection with the canal system. As the splenial elements, although true canal bones in origin, nevertheless fuse very early in their ontogenesis with the dental and angular to form complex bones, the dentale-spleniale and the angulare-spleniale, the development of these composite bones will be described later.

Preopercular. This bone develops in connection with the preopecular part of the canal. Before entering into an account of the origin of this bone, I wish to make some remarks concerning the number of sense organs in the preoperculo-mandibular line.

The number of organs in the various parts of the lateral line system in the head of Amia calva is remarkably constant. ALLIS (1889) already has pointed out the fact that he found no variations in the supraorbital line. In the supratemporal cross-commissure variations leading to the disappearance of one organ on one side as a rule correspond to an extra organ appearing on the other side, so that the total number of tube systems (and thus of sense organs) remains the same. Further he found variations in

the infraorbital and, most frequently, in the mandibular line. As the reliability of homologies founded on various bones depends to a great extent on the constancy in numbers of the sense organs—the organs themselves, as I have shown, being the actual sources of osteoblasts and thus of the bone primordia—I have examined the variation in number of the sense organs in the mandibular and preopercular line in different embryonic stages.

The investigation showed that the number of sense organs is constant only in very young stages. In stages up to a length of 12 mm therefore, the number of organs in the mandibular line amounted to 9. The most caudally situated organ is larger and will later belong to the angular-splenial bone. In older stages the number varies slightly on either side, or both. In ten different stages, from 12 to 22 mm length, the highest number was found in a 20 mm specimen still with nine organs on one side but twelve on the other. The growth in numbers is due to subdivision of the primary organs, and the result will be that more than eight organs may be connected with the dental-splenial, as well as more than one with the angular-splenial.

In the preopercular line the conditions are different. The total number of sense organs never exceeds 7, and no variations have been found. Yet in specimens smaller than 15.7 mm there are never more than 5 organs to be seen. The reason is that the last two organs (nos. 6 and 7), the ones situated most dorsally in the preopercular line, do not develop until later, that is, not earlier than in the 15.7 mm specimen. When they appear they are much smaller than the five older organs and resemble more pit line organs in shape and size. They remain different in size in all the stages I have had at my disposal.

Fig. 20. Amia calva, 12.5 mm. Lateral view of preopercular primordium. (84 × 1.) *11—14*, preopercular sense organs; vertical lines, bone; dotted, blastema.

The late development of the two dorsal sense organs in the preopercular line is of particular interest because the caudal end of the horizontal pit line of the cheek is situated ventrally to the two organs. They may be considered to be a later dorsal addition to the preopercular line, while the original, ventral part, and its prolongation rostrad, the horizontal pit line, correspond to the jugular line of the Crossopterygians.

As to the development of the preopercular bone, my material has allowed me to give a new, detailed account, in certain respects different from the description in my earlier paper. In order to simplify the following description the numeration of the preopercular organs will be based on the original, primary number of preoperculomandibular organs. Thus the most ventral of the preopercular organs will be called no. 10 and the most dorsal one no. 16.

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The first rudiment of the preopercular bone is seen in a 12 mm specimen as two aggregations of osteoblasts in connection with sense organ 12 (fig. 6). One blastema is situated rostrally to the sense organ and is elongated in dorso-ventral direction, the second one is rounded and lies ventrally to the organ. Taken together, the two blastemas correspond to a binary rudiment in, for instance, the frontal bone. In a 12.5 mm specimen the rudiments have fused ventrally to the organ 12, ossified and grown in rostro-ventral direction. The result is, that the anterior lower tip is partly underlying organ 11, whereas the posterior lower tip approaches this organ. Even in dorsal direction the H-shaped rudiment is elongated (fig. 20). In a 13.2 mm specimen the original rudiment shows the same condition, only a slight variation in the shape of the H-like rudiment being obvious. Owing to the variability in growth in different specimens it is even less ossified than was the case in the foregoing stage. But now binary aggregations of osteoblasts have developed in connection with organs 13 and 14. The rudiment under organ 13 is a little more advanced than its dorsal neighbour (fig. 21). Another sign of the variability is that in a 13.8 mm specimen (fig. 13) the first binary rudiments have not yet fused, whereas the rostral element in this pair has grown in rostro-ventral direction so much that the tip, so far not yet ossified, has extended till it has reached under the organ 10. In the next specimen of total length 15.7 great changes have taken place (fig. 22). One is that the small dorsal organs 15 and 16 are now visible. Another is that all rudiments, which have so far been separate, have now fused to form one single ossification. The double dorsal and ventral tips of the bone still indicate the binary origin. The ventral end has grown still more in rostro-ventral direction and is now situated partly under organ 10. Organs 15 and 16 have not yet become connected with the preopercular rudiment. The 16.1 mm specimen (fig. 14) shows on the whole

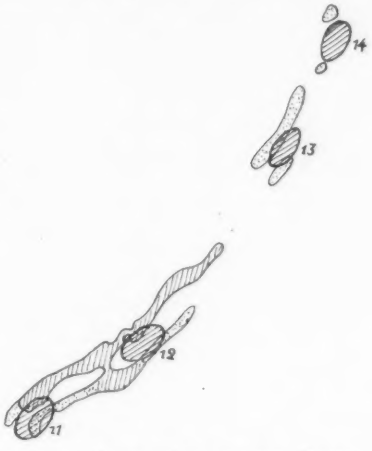

Fig. 21. Amia calva, 13.2 mm. Lateral view of preopercular primordium. (84 × 1.) Denotation as in fig. 20.

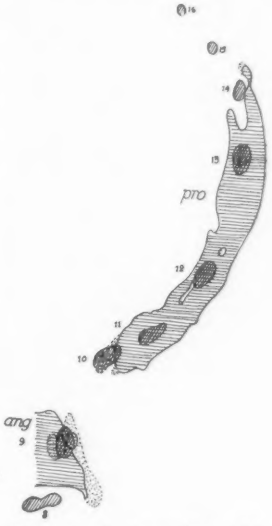

Fig. 22. Amia calva, 15.7 mm. Lateral view of preopercular and angular-splenial primordia. (42×1.) *8—16*, preoperculo-mandibular sense organs; horizontal lines, bone; dotted, blastema.

Fig. 23. Amia calva, 22 mm. Lateral view of dorsal end of preopercular. Binary blastema in connection with preopercular sense organ 16. (42 × 1.)

the same conditions as the previous stage, the only difference being that the two dorsal tips have not fused under organ 14. In the following stages the preopercular rudiment continues growing in dorsal direction and the separate tips fuse, more or less. It has not been possible to discover any separate rudiments in connection with organ 15. It seems to be included in the preopercular, simply by means of growth dorsad of the preopercular. As to organ 16, however, a special bone rudiment is formed. In the 22 mm specimen a small binary osteoblastic aggregation is situated under that organ (fig. 23). It has not been possible to follow its fate in detail for in the next stage, a 31.5 mm specimen, a single, already rather well developed preopercular has formed.

The development of the preopercular very much resembles the process of the origin of the frontal. The chief difference is only that a greater number of sense organs are involved. The preopercular thus develops from not less than four pairs of rudiments, forming respectively, in relation to the sense organs 12, 13, 14 and 16, of which the rudiment under organ 16 arises considerably much later than the rest.

Not considering the binarity of the rudiments, a fact obvious even in my earlier investigation, the details now found, may contribute to throw new light on the question of possible homologues of bones situated in the vicinity of the preopercular in fossil fishes.

It seems probable that in Cheirolepis the preopercular is formed from the rostral elements of the double row of primordia, while the caudal row leaves material for the bones x and y of Traquair.

Splenials. As already mentioned the bones in the splenial series develop in connection with the sense organs in the mandibular line. Although they form originally like all other canal bones they fuse, instead, early with the dental in the anterior and middle part of the canal, and with the angular in the caudal part, and form composite bones together with them. The dental and the angular, themselves have a quite different origin. Thus the development of the splenials will be dealt with in connection with the origin of the rest of the bones in the mandible (pages 28—36).

According to WATSON (1937) no nearer relation could be established between Acanthodians and Osteoichthyes. One of his reasons is that in the former group the sensory lateral line always runs between each two of the dermal bones, which is never the case in Osteoichthyes, where the canal is always situated in the bone. The "dermal bones" in Acanthodians are simply scales, even on the head, whereas the head of the Osteoichtyes is always covered with real bones.

Now the bones connected with the lateral line system in Amia are formed, either as binary or as single primordia. The primordia in the infraorbital line, including the rostral commissure, develop from single units and form bones which surround the neuromasts and adjacent parts of the canal system. In the same way are formed the bones belonging to the supratemporal commissure, and the bones lying further back, extrascapulars and supracleithrals. But the rest of the canal bones in the head are derived from binary primordia, as a rule developing one on each side of a neuromast. Thus, there is a fundamental and probably ancient difference in the forming of these two kinds of canal bones. Probably one primitive arrangement of bony protection of the sensory canals in scaly fishes is represented in the Acanthodians, where a line of scales is situated on each side of the canal. The ontogeny of canal bones in Amia does not contradict the possibility of a similar arrangement in the ancestors of Amia. But the conditions in the infraorbital and main body line (except in the vicinity of the first sense organ in the main body line) might represent another type of arrangement, so far not known to be represented in Acanthodians.

Probably the descendants of Acanthodians have developed larger units of bones to protect the head. The sensory canals have become embedded in the bones as a rule, either so that the bones in an original pair have fused to form one unit, or so that the canal has been surrounded by the edge of one of the two adjacent bones. In the former case the canal will be situated more or less in the middle of the single bone thus formed. In the other case the canal will lie in only one of the two original bones, and the other component, originally formed in connection with the sense organ, may either disappear or develop into a separate bone, seemingly free from the canal.

But still another possibility remains. NIELSEN (1936) found in triassic Greenland Coelacanthids (fig. 24) that the part of the supraorbital canal that runs through the nasals and rostrals does not pass through the centres of these bones. It is chiefly situated in a groove in the lateral edge of the postrostrals and frontals, a groove covered laterally by the

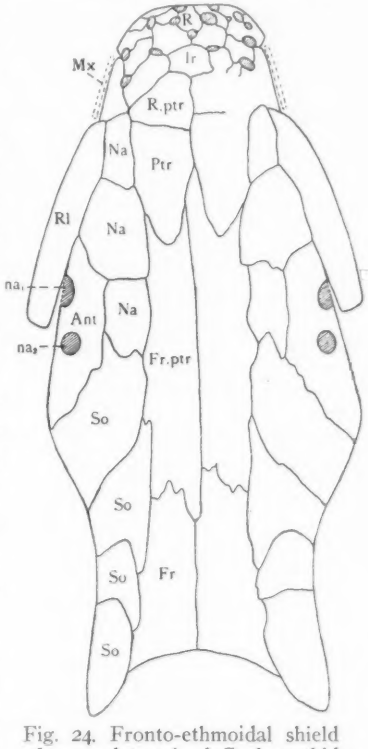

Fig. 24. Fronto-ethmoidal shield of an undetermined Coelacanthid (from Nielsen). *Fr.ptr*, frontopostrostral; *Ir*, interrostral; *Ptr*, postrostral; *R*, rostral; *So*, supraorbital; na_1 and na_2, external nasal openings. Other letters as in key, pages 47—48.

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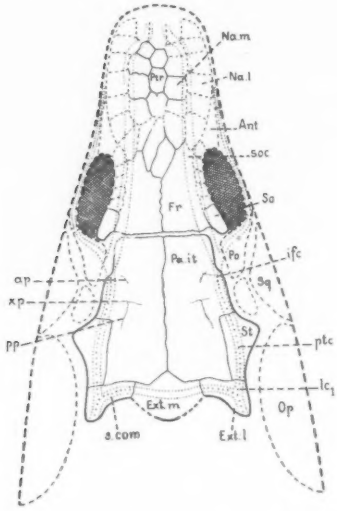
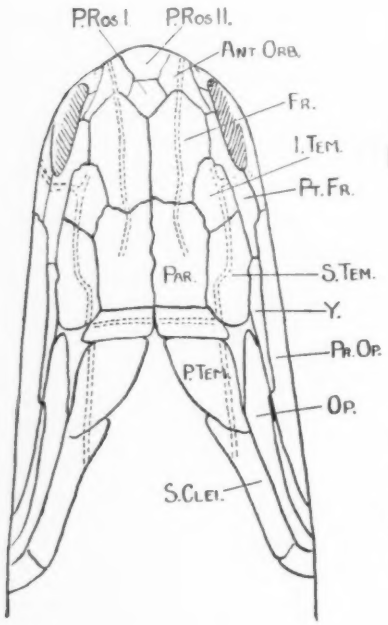


Fig. 25. Diplocercides kayseri, attempted restoration of the head in dorsal view (from Stensiö). *Ext.l, Ext.m,* extrascapulars; *Na.m, Na.l,* medial and lateral nasal plates; *Op,* operculum; *Pa.it,* parieto-intertemporal; *Sq,* squamoso-preopercular; *ap,* anterior pit line; *ifc,* infraorbital sensory canal; lc_1, cephalic division of the main lateral line; *pp,* posterior pit line; *ptc,* postotic sensory canal; *s.com,* supratemporal commissure; *soc,* supraorbital sensory canal; *xp,* pit line. Other letters as in fig. 24 and key, pages 47—48.



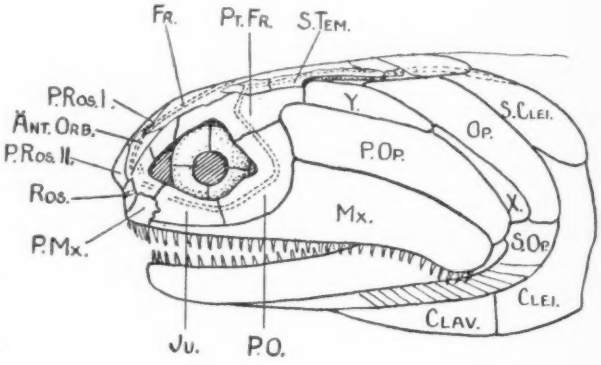


Fig. 26. Cheirolepis trailli. Left: dorsal surface of the head; right: the left side of the head (from Watson). *Ant.orb,* antorbital; *Clav,* clavicle; *Clei,* cleithrum; *Ju,* jugal; *Op,* opercular; *P.ros I* and *II,* postrostrals; *P.tem,* posttemporal; *Par,* parietal; *Pr.op* and *P.op,* preoperculum; *Pt.fr,* postfrontal; *Ros,* rostral; *S.clei,* supracleithrum; *S.op,* subopercular; *S.tem,* supratemporal; *x* and *y,* bones so called by Traquair. Other letters as in key, pages 47—48.

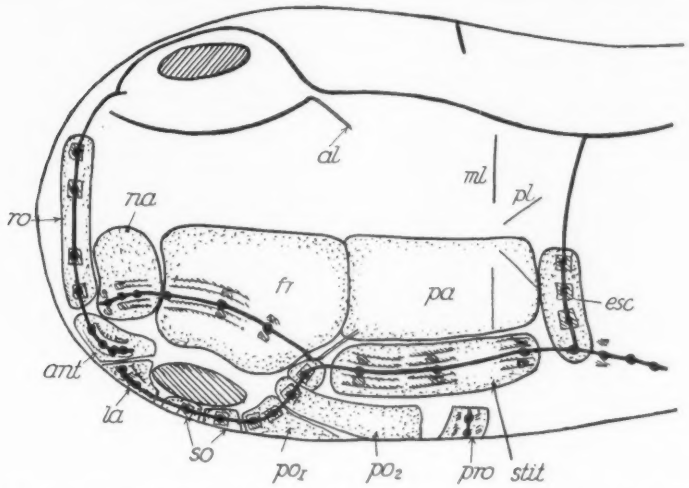


Fig. 27. Amia calva. Diagram of the head in dorsal view showing the sensory canal system and the origin of canal bones.

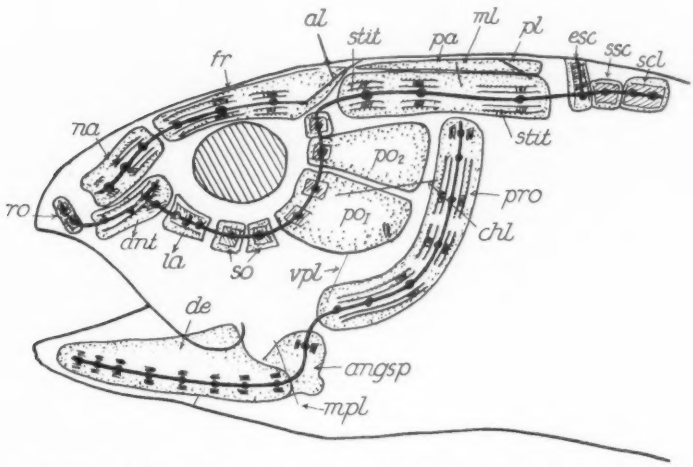


Fig. 28. Amia calva. Diagram of the head in lateral view showing the sensory canal system and the origin of canal bones.

nasals and supraorbitals, a condition corresponding to the ontogeny of these bones in Amia.

In the frontal in Amia the binary primordia fuse transversally and longitudinally around the canal to form one single bone on each side of the mid-line of the skull, while in many fossil fishes, Crossopterygians as well as Actinopterygians, the medial elements form the frontals and the lateral ones the supraorbitals.

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In the same way the binary nasal primordia in Amia fuse and form the nasals, while in the case of the Coelacanthids, mentioned above, the lateral elements form the nasals (one or several on each side) and the medial elements the postrostrals. In the Devonian Diplocercides (STENSIÖ, 1937), on the other hand, (fig. 25) there seems to be a double row of nasals as well as a median row of single postrostrals. The lateral nasals are the homologons of the postrostrals of NIELSEN's material, and their vis-à-vis, situated medially to the canal, correspond to NIELSEN's postrostrals. The so-called postrostrals in the mid-line should then be interpreted as spacefilling, anamestic bones (WESTOLL, 1936), impossible to homologize with more fixed morphological elements.

In Cheirolepis (WATSON, 1925) the rostral commissure (fig. 26) passes through the two rostrals and continues backward in an antorbital (lacrimal, WATSON), where the canal has a dorsal branch, then through the lacrimal, which is possibly fused with an infraorbital element (jugal, WATSON), further through a comparatively large postorbital to a dermosphenotic, probably fused with the hindmost supraorbital, eventually to turn backward again in the intertemporal. The supraorbital canal begins in the nasal (antorbital, WATSON), passes through the frontal and ends in the parietal. Above the eye between the lacrimal and the dermosphenotic is a small, free supraorbital, but, as already pointed out, there may be supraorbital elements present in the anterior part of the dermosphenotic.

B. BONES NOT DEVELOPED IN CONNECTION WITH THE SENSORY CANAL SYSTEM.

Although the parietal develops differently from the canal bones proper, I have preferred to describe its origin together with these ossifications. It is regarded at least in the paleontological literature as more or less related to the canal bones, as it is supposed to develop in some connection with pit lines. Above has been shown that pit organs, at least in Amia, do not play any part in the formation of the parietal, yet it arises, if not in genetical, at least in topographical relation to pit lines. In my opinion, the parietal is to be looked upon as a secondary product of the supratemporo-intertemporal part of the canal system.

This chapter will first deal with a number of bones, all developing in the same way and all drawing their material from the same histogenetic sources. The bones are as follows: maxillary, supramaxillary, ecto- and entopterygoid, dental, angular, prearticular and parasphenoid. They have their origin in different parts of the mesenchymatous tissue that forms the walls of the mouth cavity. In this mesenchyma the matrix of the various bones is visible

in early stages as denser nucleated regions, forming more or less rounded, sometimes more flattened, elongated parts. They are so indistinctly defined that it is impossible to represent them in a reconstruction. To a certain degree those preblastemas of the bones are connected with each other, indicating their common origin. These connections will be mentioned in the descriptions of the development of respective bones. The investigation of the origin and earliest development of the preblastemas falls outside the range of this paper. Besides, it involves new problems, not possible to solve on the basis, only of an examination of the early embryonic development of Amia calva.

Common to all these bones is that they do not develop in connection with teeth. Many of them will be tooth-bearing, but in those cases teeth develop independently and fuse later with the bones.

Maxillary. The first traces of an ossified primordium of the maxillary are discovered in a 9.5 mm specimen. In the maxillary fold there is a cylindrical, rod-like blastema. Its centre is formed of the narrow, needle-like, ossified maxillary, that occupies about 2/3 of the length of the blastema. In a still younger specimen, measuring 9.2 mm, no ossification had taken place in the blastema. In these early stages the maxillary blastema gradually changes rostrad into the above mentioned less densely nucleated aggregation of cells, which forms a sort of preblastema. This maxillary preblastema, in its turn, is connected with a similar cellular aggregation round the rostral end of the palatoquadrate.

In the nearest following stages the maxillary increases in length, still keeping its needle- or rod-like shape. In the 13.8 mm specimen the caudal end begins to develop a dorsally directed lamella (fig. 13), and in the 16.1 mm specimen it has practically assumed the shape it has in the adult (fig. 14).

Supra-maxillary (jugal of some authors) develops, unlike the maxillary, very late. In the 31.5 mm specimen it exists as a short, bony plate, situated in the caudal end of the maxillary fold above the end of the maxillary. Due to the gap in my material I am unable to give a more detailed account of its origin. In the 22 mm specimen, and earlier, there is no trace of the bone, not even in shape of a preblastema, yet it seems probable it is derived from the same source as the maxillary.

Ectopterygoid. Already in a 9.2 mm specimen the blastema of the ectopterygoid is differentiated from the mesenchyma in the shape of a tape-like elongated aggregation of cells. The primordium is situated in the lining of the roof of the mouth cavity, along the ventral side of the palato-quadrate. This cartilage has not yet reached the tip of the trabecula but is connected with it by means of prochondrial tissue. The ectopterygoid blastema extends from the rostral end of the chondrified part of the palato-quadrate and backward to a point slightly rostrally to the joint between the quadrate part of the cartilage and the Meckelian cartilage. Here it changes gradually into the already mentioned

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preblastematic tissue, which, in its turn, continues rostrad and passes into the blastema of the prearticular primordium. The joining place of the two primordia on the inner side of the Meckelian cartilage is situated on a level with the corresponding meeting place of the caudal ends of the caudal continuation of the maxillary preblastema, and the caudal end of the dental blastema. Both these joining places are connected with each other by means of a streak of preblastema, which runs across the caudal part of the Meckelian cartilage. The blastematic primordia of the dentary, the ectopterygoid and the prearticular thus meet over the caudal end of the Meckelian cartilage. It might be added that the growth of the coronoid process takes place from the point where the blastemas meet.

In a 12 mm specimen (fig. 29) the caudal connection of the ectopterygoid primordium with the still existing blastematic aggregation on the caudal end of the Meckelian cartilage has dissolved. The caudal part of the ectopterygoid primordium has already ossified, whereas the rostral part still has the character of a well defined blastema. The anterior end of this blastema, however, is not so sharply outlined. It changes gradually rostrad into the same kind of less densely nucleated blastema as forms the above mentioned tissue on the posterior end of the Meckelian cartilage. In this place the anterior end of the entopterygoid has its origin.

In these early stages no tooth rudiments are yet visible in the area of the epithelium of the palate situated over the ectopterygoid primordium. In a 15.7 mm specimen, however, tooth rudiments are beginning to develop in the epithelium over the bone. In that stage, but not earlier, the primordium has ossified in its whole length. Yet the very tip of the anterior end is still connected with the, so far, unossified primordium of the entopterygoid by means of a streak of blastema. Not until the 22 mm stage teeth begin to fuse with the lateral edge of the rostral end of the bone.

Entopterygoid. As seen from the description of the formation of the ectopterygoid, the entopterygoid develops in the same way. In early stages (fig. 29) its rostral end, as already mentioned, is connected with the end of the ectopterygoid on the ventral side of the palato-quadrate. Only a short part of the rostral end lies in contact with the cartilage. The larger part of the blastema is situated in the mesenchyma in the roof of the mouth. Unlike the ectopterygoid, ossification does not begin from the caudal end. The reason is obviously, that, whereas the blastema of the ectopterygoid has its oldest part caudally, the case is the opposite with the entopterygoid. Yet it is not in the rostral tip that bone is first formed, but a little further caudad, where the primordium leaves its contact with the palato-quadrate. Ossification begins in the 16.1 mm specimen.

Dental (dentale-spleniale). The dental is a composite bone consisting partly of a dental component developed in the same way as described above, partly

of a series of splenial elements forming along the mandibular canal, in principle like the rest of the canal bones.

The first ossified rudiment of the dental is seen in a 9.5 mm specimen as an elongated, somewhat gutter-shaped bone plate on the lateral side of the Meckelian cartilage. Its caudal end is situated on a level with the still practically undeveloped processus coronoideus. Like the maxillary in this stage it is enclosed in a thin coating of cells. Caudally the primordium still consists of unossified blastema, that is cloven in one dorsal and one ventral branch. The former is connected with the earlier mentioned aggregation of blastema cells round the tip of the proc. coronoideus by means of the usual, more sparsely nucleated tissue. The ventral branch continues backward along the processus retroarticularis of the Meckelian cartilage.

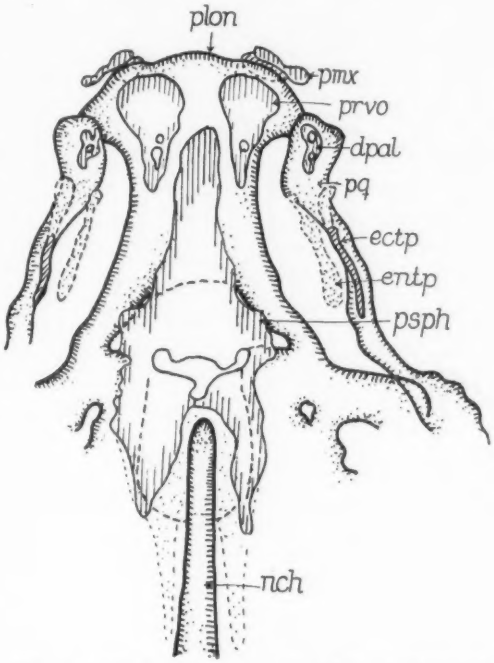

Fig. 29. Amia calva, 12 mm. Ventral view of anterior part of cranium with bone primordia. (40 × 1.)

Rudiments of teeth with calcified tips are developed already in this stage, yet they show no connection with the dentary. As a matter of fact three tooth rudiments are already visible in a 7.5 mm specimen (fig. 31), in shape of well developed vesicles. In the 9.5 specimen (fig. 30) another tooth rudiment has formed in front, and one behind the first three rudiments. Thus there are in all five on each side of the mandible.

Splenial elements are not formed in this stage, although the sense organs in the mandibular line are well developed. They are still situated on a level with the surface of the ectoderm. The sense organs show the same capacity for producing osteblasts, migrating into the mesenchyma. Immediately inside the basal membrane has formed a ribbon-like layer of more densely nucleated mesenchyma where the canal will eventually develop.

The primordium of the dental ossifies apparently in one piece. Yet it shows what might be called an indication of a subdivision in one anterior and one posterior half. In a reconstruction of a 9.5 mm specimen (fig. 30) there is seen a quite unmistakable narrowing of the bone on both sides. To

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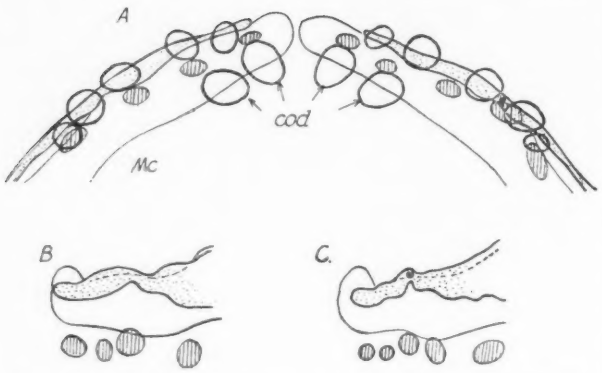

Fig. 30. Amia calva, 9.5 mm. A: dorsal view of mandible with dental primordium, B: lateral view of left mandible, C: lateral view of right mandible. (84 × 1.) White circles, tooth rudiments; vertical lines, mandibular sense organs; dotted, bone.

the right in the illustration the bone is not only narrower, it is even incompletely ossified, as there are small perforations left in it. These conditions show in the horizontal as well as in the lateral reconstruction. This narrow place can be located on both sides as regards its position relative to the sense organs and to the tooth rudiments. As fig. 30 shows it is situated between the sense organs 3 and 4 and between the tooth rudiments 3 and 4.

In itself this condition might not be regarded as in any way remarkable, but it can be traced quite distinctly in the following stages up to the 16.1 mm specimen. Now it is known that the Meckelian cartilage in Acanthodians was divided in one anterior and one posterior part, whereas no dental was developed. The Acanthodians are reckoned as possible progenitors of all Osteichtyes. From that point of view the question arose as to whether a similar subdivision of the Meckelian cartilage could also be found in Amia. Reconstructions of the Meckelian cartilage in specimens measuring 7.5 and 8.0 mm, the earliest where the cartilage has formed, and in 9.0 and 9.5 mm specimens, are seen in figs. 30 and 31. No sense organs are formed so far, but rudiments of dentary teeth are already developed. In the 7.5 mm specimen the cartilage still has a transverse position and the proximal end still consists of prochondrial tissue. There is no gap to be seen between the two parts. That is not the case in the 8 mm specimen, either, yet the cartilage might be considered as consisting of one proximal and

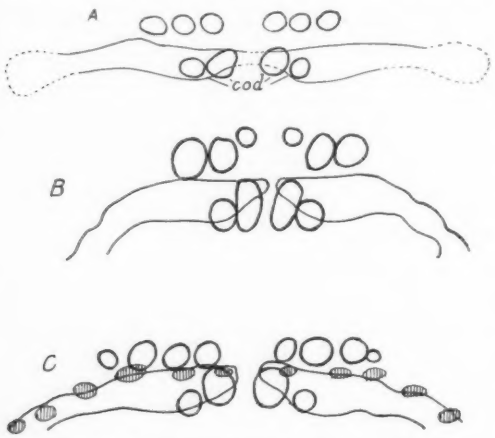

Fig. 31. Amia calva. Dorsal view of Meckelian cartilage. A: 7.5 mm specimen, B: 8.0 mm spec., C: 9.0 mm spec. (63×1.) Denotation as in fig. 30.

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one distal part, the boundary between both situated behind (lateral to) the third tooth rudiment.

In a 10 mm specimen the ossification of the dental has progressed caudad. While the caudal part shows a tendency to spread in dorso-ventral direction, the rostral part grows under the cartilage and develops a horizontal flap, or lamella, in this stage still consisting of blastematic tissue, only. It is situated entirely anteriorly to the narrow part of the dental mentioned above.

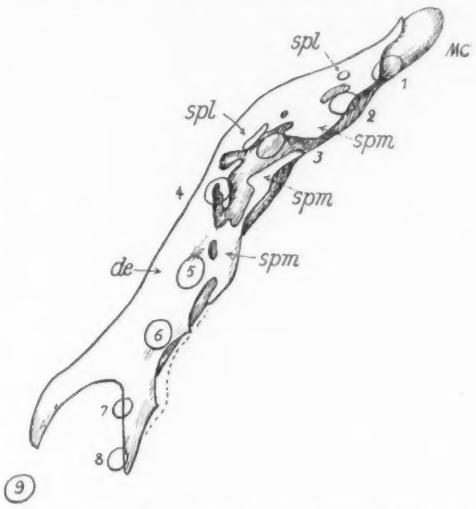

Fig. 32. Amia calva, 12 mm. Ventral view of right mandible showing dental to the left and splenial primordia to the right. (63×1.) White circles 1—9, mandibular sense organs.

The development of the dental in the ensuing stages is rather complicated, and characterized by the simultaneous development of splenial elements. From now the bone changes from a mere dental to a dentale-spleniale. The backward prolongation continues at the same time. As mentioned above, 8 primary sense organs belong to the mandibular line and take part in formation of the splenial part of the composite bone. The general scheme of development of the splenials runs as follows: In connection with each sense organ there develops one binary splenial primordium. It consists of one medial and one lateral element. The medial element ossifies as a continuation of the medial or (further caudad) ventral edge of the dentary. The lateral element, on the other hand, ossifies as an elongated disc of bone which becomes attached lengthwise to the dental laterally or (further caudad) dorsally to its respective sense organ. The growth of the dentale-spleniale is illustrated in figs. 30—33, and 36, as well as in the microphotographs, figs. 34 and 35.

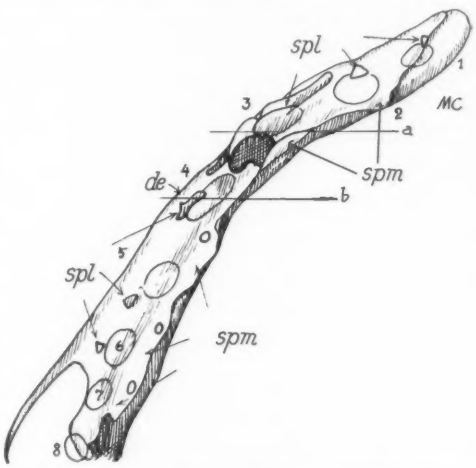

Fig. 33. Amia calva, 13.8 mm. Ventral view of right mandible. (63 × 1.) *a*, position of cross-section shown in fig. 34; *b*, position of cross-section shown in fig. 35. Other letters as in fig. 32 and in key, pages 47—48.

The conditions in a 12 mm specimen may be understood from fig.

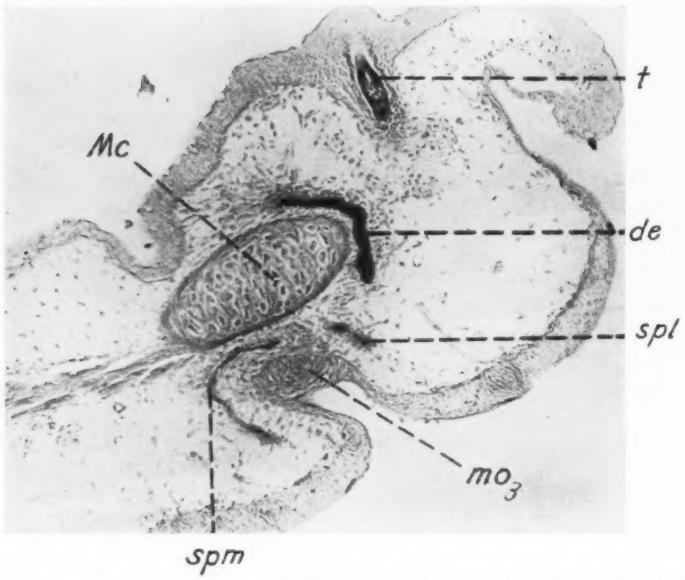

Fig. 34. Amia calva, 13.8 mm. Cross-section of mandible (cfr fig. 33). mo_3, mandibular sense organ 3. Microphotograph.

32, showing a reconstruction of the mandible seen from the ventral side. Medial elements are already developed in connection with all sense organs, except the first, and possibly the last. The attachment of the medial elements belonging to sense organs 2 and 3 is accomplished, and only two small foramina indicate that the process is not yet entirely finished. The medial elements developing in connection with organs 4 and 5 are partially free, because they are situated at the narrow part of the dental. Thus they have to form a bridge over the gap between the overhanging medial edges of the distal and the proximal part of the dental, which explains why they, unlike the rest of the medial elements, do not become attached to the edge of the dental. As to the medial elements forming in connection with sense organs 6 and 7, they are developed as two jags on the edge of the dental with a deep indentation on each side. No splenial elements seem to have formed so far in connection with sense organ nr. 8. A lateral element is developed in shape of a short tag of bone in connection with organ 2, and another, considerably longer, with organ 3. No other lateral elements are formed in this stage.

The changes that have taken place in a 13.8 mm specimen are illustrated in fig. 33 and the microphotographs, figs. 34 and 35. The dental-splenial has apparently broadened considerably. This is due to the growth of the rim, now formed medially by the medial splenial elements. The gap in the dental is thus bridged over entirely. The enlargement of the posterior medial elements

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has caused the inner edge of this part of the bone to form a straight line. An indication of the incorporation and growth of the splenial elements in this posterior half of the bone is a series of three perforations. This part of the splenial edge of the bone has now reached the stage where the anterior part of the bone exists, as shown in the 12 mm specimen. In that part the former perforations are now filled in. In the caudal, medial (or ventral) end of the bone, on the contrary now, the typical indentations show, due to the development of medial splenial elements in connection with the last two sense organs. Lateral elements have formed in connection with all sense organs except at no. 7 and no. 8. The former bone tag in connection with organ 3 has grown distally as well as proximally. Distally it develops a long process pointing towards its distal neighbour, and proximally it has reached the caudal side of the gap in the dental. The bridge over this gap is thus formed by the lateral as well as by the medial element. Together they form a gutter-shaped part, where only a foramen at the bottom bears witness to its double origin. The microphotograph, fig. 34 shows a cross-section on a level with this foramen. In the photograph the bone apparently consists of three elements. Seen from left to right the bones are the medial and the lateral splenial element and the dental at its narrowest part. Further to the right, and upward, is a developing tooth. The sense organ is no. 3. The microphotograph, fig. 35, shows a cross-section further back through sense organ 4. The S-shaped bone is the dental and the medial splenial element. The lateral element shows a little projecting tab.

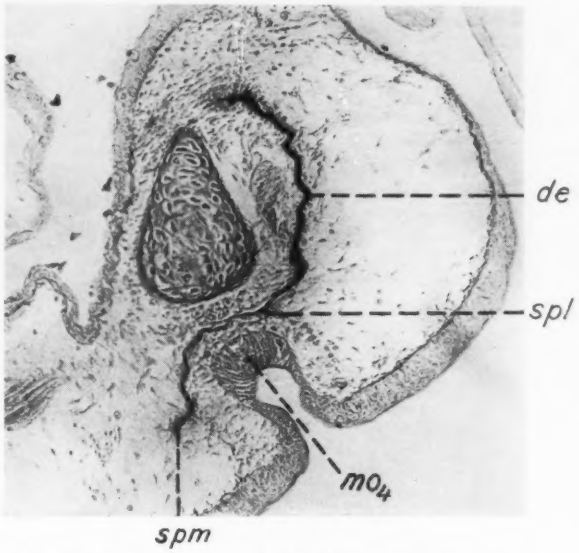

Fig. 35. Amia calva, 13.8 mm. Cross-section of mandible (cfr fig. 33). mo_4, mandibular sense organ 4. Microphotograph.

In a 16.1 mm specimen (fig. 36) the dental-splenial has developed into a fairly good-sized bone. Neither perforations nor indentations indicate the origin of the medial edge of the bone. Due to variations in development the splenial elements connected with sense organ 8 have not come into contact with the dental in this specimen, at least not in the side selected for reconstruction, therefore they show the interesting condition of still forming a binary

Fig. 36. Amia calva, 16.1 mm. Ventral view of right mandible. In connection with sense organ 8 a blastematic binary splenial primordium. (63 × 1.)

blastema under the epidermis. The lateral elements of organs 3 and 4 have joined and continue backward and forward as long, pointed processes, free from the dental. Together with the medial edge of the bone, which is curved outward, they form a broad gutter for the sensory canal. The foramen at the bottom of this gutter still exists, but has shrunk considerably.

The development from this stage on does not afford anything of special interest. The lateral elements grow in length and fuse, thus adding to the comparatively short gutter in the previous stage. Simultaneously the bone grows in thickness and forms the usual lamellas. The first indications of the formations of lamellas are already seen in the 16.1 mm specimen.

Angular (angular-splenial). As already mentioned this bone originates from the same preblastema in the mandible as the dental, the supra-angular and the prearticular. This refers only to the angular part. The splenial part is formed from the sense organs in the angular section of the mandibular canal (cfr. figs. 6, 13 and 14).

In a 9.9 mm specimen the primordium of the angular is only to be distinguished with some difficulty in the comparatively densely nucleated tissue, that surrounds the caudal end of the processus retroarticularis, the still very little developed processus coronoideus, and the blastema that forms the caudal end of the dental primordium. In a 10 mm specimen this last mentioned part has separated from the perichondrium. A thin coating of cells is left on the cartilage ventrally of the proc. coronoideus. It is situated immediately on the perichondrium, chiefly in the ventral part of the cartilage, but extends up onto the lateral part as well. That is the primordium of the angular, still in the blastematic stage. In a 12 mm specimen it has ossified as is shown in fig. 6. The further development is seen from figs. 13 and 14.

The mandibular line follows the mandible in a fairly straight line along

the dental. Behind the caudal end of this bone it makes a sharp dorsal curve over the angular bone and then continues in a dorso-caudal direction as the preopercular line. The short angular section of the sensory line contains in all early stages only one sense organ. This organ differs very markedly from the mandibular organs not only because of its position but even because of its larger size.

In relation to this organ is formed the binary primordium of one splenial element in the same way as is usual for the development of canal bones (fig. 22). Like the splenials, which form in the dental part of the line, even this primordium fuses with the underlying bone simultaneously with its formation. In the case of the dental splenials, one element in each pair of splenials is comparatively more independent, namely the lateral one, the other, median bone forming more like a continuation of the edge of the dental. Here the ventral bone is comparatively free, whereas the dorsal bone is situated as a continuation of the dorsal rim of the angular.

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In the 16.1 mm specimen, where there are, as already mentioned, 9 sense organs on one side of the dental part of the mandibular line, there are on the same side two sense organs in the angular part. The second organ lies dorsally to the first (and original) one. From both develop binary, ossified primordia, subsequently to fuse with the angular. In a 22 mm specimen there are also three splenials, attached to the angular, formed from three sense organs.

The development of the various bones on the outside of the mandible of Amia results in formation of three independent bones, the dental, the angular and the supra-angular. The dental will later connect with teeth but develops without any relation to them. As to the supra-angular it forms comparatively late during the ontogeny but is nevertheless a product of the same tissue as the two other bones. Besides these three bones there is the series of splenial bones attached to the dental. The ontogeny of the splenial series seems to indicate an earlier phylogenetic stage, where the mandible consisted of the three bones mentioned above and a series of free splenials. No such fossil fish is known, however.

On the outside of the mandible of the carboniferous and permian Rhipidistian Megalichthys there are five separate bones (fig. 37). The most anterior is (with the names used for instance by WATSON) the splenial, behind it the postsplenial, then the angular and, caudally, the surangular. The edge of the mandible is formed by the dentary. No doubt the dentary is the homologon of the dental of Amia. Whether the surangular and the angular are the homologons of the similarly named bones in Amia is less certain. Their surface indicates the presence of a sensory canal. Thus they are, doubtlessly, formed like splenials, as are also the first two bones. In any

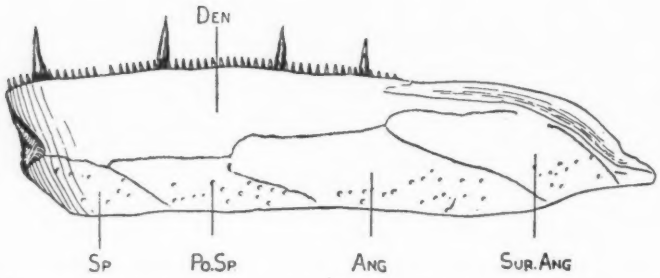

Fig. 37. Megalichthys. Lateral view of left mandible (from Watson). *Den*, dentary; *Sp*, splenial; *Po.Sp*, postsplenial; *Ang*, angular; *Sur.Ang*, supraangular.

case there are four separate bones of splenial origin in Megalichthys. The splenial and postsplenial are probably purely splenial bones. As to the name angular it seems more suitable to reserve it for the bone called surangular. A real surangular, if it exists in Megalichthys, would probably be covered by other bones and thus be invisible in the picture. Then the so-called angular might be a third splenial bone. Finally, as the dentary seems to be free from splenials, that might be the case even with the real angular, if such a bone exists in Megalichthys, and in that case even the so-called surangular would be a real splenial element. Thus it is possible there are four such bones in this fish. The number of bones in the various parts of the sensory canal system may vary in different fishes for several reasons. One—and the most obvious—is that the number of sense organs is not the same. Amia begins with 8 dental organs (and one angular) but later on develops more organs in the mandibular line. In other fishes the number is different, so it is not improbable in Megalichthys, as well as in other Rhipidistians, there were free splenials, even if their number was not the same as in Amia.

Prearticular. This is the large bone covering the inside of the mandible. It has been given various names and been reckoned as one bone in the coronoid series or in the splenial series. As will be shown later, the coronoids develop in a different way, and as to the term splenials it should be reserved for the canal bones forming along the mandibular line and fusing with the dental and the angular.

The prearticular develops from a blastema extending as a ribbon-like aggregation of cells along the inside of the Meckelian cartilage near its dorsal surface and in the narrow space between the cartilage and the epithelium of the inside of the lower jaw. It ossifies rather late. In a 13.8 mm specimen the anterior end, situated about half-way between the tip of the Meckelian cartilage and the quadrate joint, has ossified in the shape of a narrow strip of bone. It continues caudad as a ribbon-like blastema. In a 17 mm specimen it extends like a thin, bony blade along the posterior two thirds of the cartilage.

Supraangular. The origin of this bone is the blastematic tissue at the proc. coronoideus of the Meckelian cartilage. This aggregation of cells is visible already in a 9.5 mm specimen. A real blastema, however, is not formed until considerably later and is seen in a 22 mm specimen. It is situated on the lateral part of the coronoid process between the tip of this process and the dorsal branch of the caudal end of the dental, and extends caudad along the processus retroarticularis. The gap in my material does not allow me to determine, exactly, when ossification takes place. In a 31.5 mm specimen a real bone has developed.

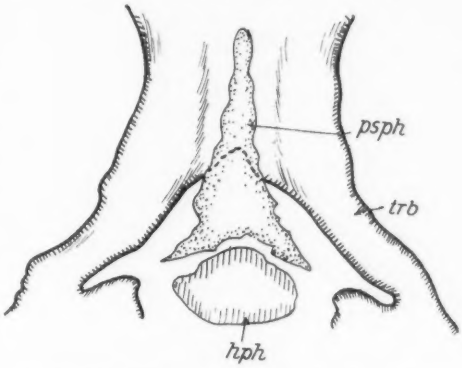

Fig. 38. Amia calva, 9.5 mm. Ventral view of trabecles and commissura trabecularis showing parasphenoid primordium. (83 × 1.)

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Parasphenoid This bone has its origin from the same kind of diffused blastema-like tissue, that I have called preblastema. The source of the parasphenoid is the mesenchyma situated between the anterior parts of the trabecles. Already in a 9.5 mm specimen the primordium of the parasphenoid has ossified (fig. 38) in the shape of a thin, triangular, plate. In this stage the trabecular commissure has formed as well. The primordium of the parasphenoid lies with its anterior half underneath the commissure, while the posterior half is situated under the fenestra basicranialis. The caudal side of the triangle is slightly curved rostrad and lies immediately in front of the hypophysis.

No bone is developed behind the hypophysis in these early stages but a blastema is forming on both sides of the anterior end of the notochord, yet too indistinctly to be recorded in a reconstruction. In a 10.4 mm specimen (fig. 39) the blastema has ossified on both sides of the notochord. The result is a thin, bony plate on each side, connected to the right and to the left of the hypophysis with the older part of the parasphenoid by means of a very thin and indistinct bony commissure. On one side of the hypophysis this connection is very narrow,

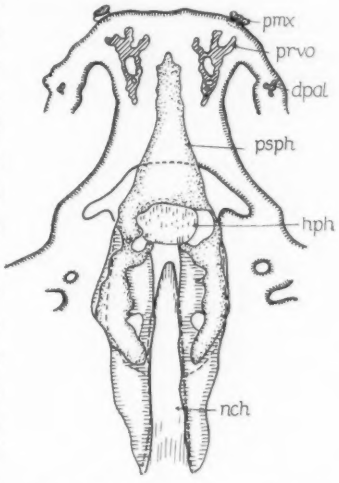

Fig. 39. Amia calva, 10.4 mm. Ventral view of anterior part of skull showing bone primordia. (42 × 1.) Dotted, ossified part of parasphenoid; horizontal lines, blastematic part of parasph.; oblique lines, other bone primordia.

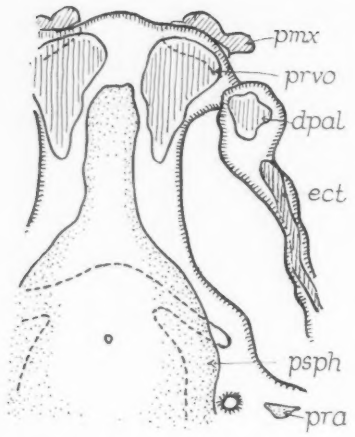

Fig. 40. Amia calva, 13.8 mm. Ventral view of anterior part of cranium. (42 × 1.)

on the other pierced by several perforations due to imperfect ossification.

It does not seem improbable that this caudal part of the parasphenoid might be considered a pair of independent primordia. I have not been able, however, to find a stage, where they are entirely free from the anterior part of the bone.

In a 12 mm stage (fig. 29) the connections between the anterior and the posterior parts have broadened, and a bone commissure has formed between the two posterior elements. Still there is a rather large fenestra hypophyseos left open. No traces of processus ascendentes are to be seen in the stages now mentioned. In the 13.8 mm specimen the parasphenoid has broadened and, except the small foramen hypophyseos, the polar fenestra is entirely covered. In this stage the first rudiments of proc. ascendentes appear. They do not develop from the parasphenoid itself but form as independent primordia. Dorsally to the foramen palatinum and on the anterior part of the auditory capsule, between the cartilage and the caudal wall of the middle part of the spiracular canal a little bone plate is visible on each side (fig. 40). They are the primordia of the proc. ascendentes. Their further development and final attachment to the body of the parasphenoid—in the 16.5 mm specimen—is shown in fig. 41.

Stensiö (1932) has pointed out, that there are two different pairs of proc. asc. in fishes, one anterior and one posterior. In Amia the anterior pair is developed. As is shown, they form as separate bones, which grow independently and later fuse with the parasphenoid. Under such circumstances it might be expected that separate parasphenoid wings, existing as free bones, should be found in extinct fishes, such as Crossopterygians or Paleoniscids. So far that is not the case. On the contrary the so-called centre of growth of the parasphenoid seems to indicate an original formation in one single piece of the bone. From the centre of growth, ridges radiate backward and forward, as well as sideways on to the wings.

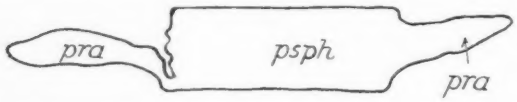

Fig. 41. Amia calva, 16.5 mm. Middle part of parasphenoid showing the fusion of the corpus of the bone and the proc. ascendentes. (42 × 1.)

Now it is doubtful whether a centre of growth—a term chiefly used by paleontologists—should be assigned any more importance than the word implies. It seems

probable that the ridges are formed in accordance with mechanical laws like, for instance, the lamellas in spongious bone. A bone like the supratemporo-intertemporal in recent fishes, as well as in extinct ones, shows—according to the age of the specimen—a more less well marked centre of growth. Yet, if one is to believe in embryological evidence, there is no doubt that the bone in question has developed from one binary supratemporal component, and from one binary (or two) intertemporal components. In the adult fish there is no trace whatever to be seen of the ontogenetic, far less of the phylogenetic story of the bone. The tale of its ontogeny can only be read in comparatively early embryonic stages, and will be wiped out very soon, and as to the phylogeny it is only a matter of scientific judgement.

Some resemblance with the conditions in extinct fishes is found in the shortness of the early primordium of the parasphenoid. In Coelacanthids this bone was very short, partly due to the separation of the skull in an anterior and one posterior part allowing a certain degree of flexure. The parasphenoid of these fishes thus belongs entirely to the front half of the skull. Further the parasphenoid of the Crossopterygians had no processus ascendentes, a condition corresponding to the parasphenoid in a 9.5 mm Amia.

Even in various Paleoniscids the parasphenoid was short and triangular (ALDINGER, 1937), though not homologous with the primordium of the bone in the 9.5 mm Amia, as both pairs of proc. ascendentes were developed.

The remaining dermal ossifications in the skull of Amia form a group of their own as far as their development is concerned. These bones are the prevomer, the dermopalatinum I and II, the coronoids and the premaxillary. The material of the primordia of these bones is the same diffused, comparatively densely nucleated areas in the mesenchyma, that formed the blastemas of the bones enumerated in the foregoing part of this chapter. So far there is no principal difference between, for instance, the origin of the prevomer and the maxillary. The dissimilarity in development concerns chiefly the method of ossification, due to the fact that the bones of the prevomer type have early relations to teeth, while the tooth-bearing bones belonging to the former group become later connected with teeth. For the sake of brevity I call the group of bones comprising the maxillary, the pterygoids etc., the maxillary group and the one mentioned above including premover, dermopalatinum etc., the prevomer group.

As already described the development of the primordia of the bones belonging to the maxillary group takes place from a blastema easily distinguishable from the rest of the mesenchyma, although not so clearly outlined as the blastemas of the canal bones. The primordia of the latter bones form after migration of cells from the ectoderm in a mesenchyma generally very sparsely nucleated, where the aggregations of osteoblasts contrast very well.

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It is only in places where narrow space and the vicinity of other tissues combine to blur the picture, as is the case for instance in the anterior end of the mandible, that some difficulty may arise in outlining the blastemas. The primordia of bones of the maxillary type form in places where the mesenchyma seems to be more densely nucleated than otherwhere. This tissue, or preblastema, as it might be called, not yet being so well outlined as to be named real blastema, concentrates gradually to form the primordium of the bone.

Ossification takes place very much in the same way in the blastemas of the canal bones as in the developing bones of the maxillary type. In the middle of the blastema, bone is deposited, often in one place, sometimes in several, and from these centres ossification spreads, still in the middle of the blastema, until a confluent disc, or rod, is formed. No visible, external agendum causes the ossification, which begins, as a rule, in the part first definitely formed.

In the blastemas of the bones belonging to the prevomer group the process is different. As will be described in detail later, the first parts to ossify are the parts of the blastema, situated immediately under tooth rudiments. Thus ring- or horseshoe-shaped small deposits of bone are the first ossified parts to be seen (fig. 42). The next stage is the growth of those rings or horseshoes to slightly larger pieces which fuse to form the first rudiment of the bone, although still showing the shape of the original components (fig. 39). New rings, or horseshoes, might be added as the contribution of more teeth joining the rudiment. The primordium then begins to grow round the edges from bone supplied by the original blastema. Little by little the first components get filled out with bone (fig. 29 and fig. 40) and a solid plate is formed. Only then the tooth itself fuses to the bone. It might be added that the apex of the tooth has ossified like a needle, or tag, of dentine, already before the ossification of the basal part. Generally the denticles are the first hard parts to be formed in an embryo of Amia and are to be seen before the appearance of any bones.

Bones developing in connection with teeth are found at the anterior end of the trabecles, of the palato-quadrate and of the Meckelian cartilage. They are the prevomer and the premaxillary, the dermopalatina and the coronoids, respectively.

Prevomer. Vomer, or prevomer, as the bone is called in Amia, where there are two bones situated one on either side of the anterior ventral part of the orbito-nasal plate, develops in the following way.

In a 8.2 mm specimen the anterior ends of the trabecles are still free from each other, and the coming planum antorbitale is only indicated in the shape of faintly differentiated prochondrial tissue.

The tips and the lateral and ventral parts of the trabecles are covered with densely nucleated mesenchyma. Teeth are already developing in shape of comparatively large, oval vesicles in the ectoderm of the palate. They are separated from the trabecles and their covering tissue by ordinary mesenchyma. Some of the most advanced teeth have formed a dentine point. No sign of the prevomera is so far to be seen.

In a 9.2 mm specimen a commissura trabecularis has formed. The tissue referred to above as densely nucleated has differentiated in a sort of blastema, which covers a part of the anterior end of the trabecle ventrally and forms a small dorsal area as well. There still are no ossifications to be seen, except in the tooth rudiments.

In a 10 mm specimen (fig. 42) the same conditions are better accentuated. The diagram shows the outlines of the blastema, still rather indistinct, that covers the lateroventral part of the anterior end of the planum antorbitale, now taking shape. The anterior part of the blastema overlaps the tip of the cartilage and forms a dorsal tab in the dorsal surface.

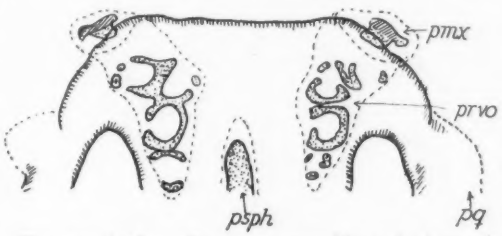

Fig. 42. Amia calva, 10.0 mm. Ventral view of anterior part of cranium. (84 × 1.) Blastematic tissue surrounded by dotted lines.

The teeth have developed rather quickly. Large dentine cones have formed and the entire vesicle has grown in size, till it has reached contact with the blastema. At the point of contact ossification begins. The earliest bony parts are horseshoe-shaped pieces, sometimes broken up in smaller elements. As is seen from the cross-section, fig. 43, the tooth bases are still connected with the cone of the tooth solely with odontoblastic tissue. In fig. 42 there are ossifications under four teeth to be seen on each side.

In a 10.4 mm specimen the separate ossifications have fused to form one bone on each side (fig. 39) of the anterior part of the planum antorbitale. The original elements still show plainly. The caudal parts have grown because of addition of still more teeth. This is seen in the right side of the diagram. In a 12 mm specimen (fig. 29) the bone has grown considerably. In this stage, but not earlier, the ossification of the prevomeral teeth is complete. The microphotographs fig. 44 and fig. 45 show two cross-sections through the prevomer. In fig. 44 is seen a complete tooth in the anterior part of the bone, in fig. 45 the ossification in the caudal addition (cfr. fig. 29). Up to this point each tooth except the tip has consisted of non ossified odontoblastic tissue.

Although it may seem as if the old HERTWIG theory of the origin of tooth-bearing bones from tooth fusion were to be verified, the explanation

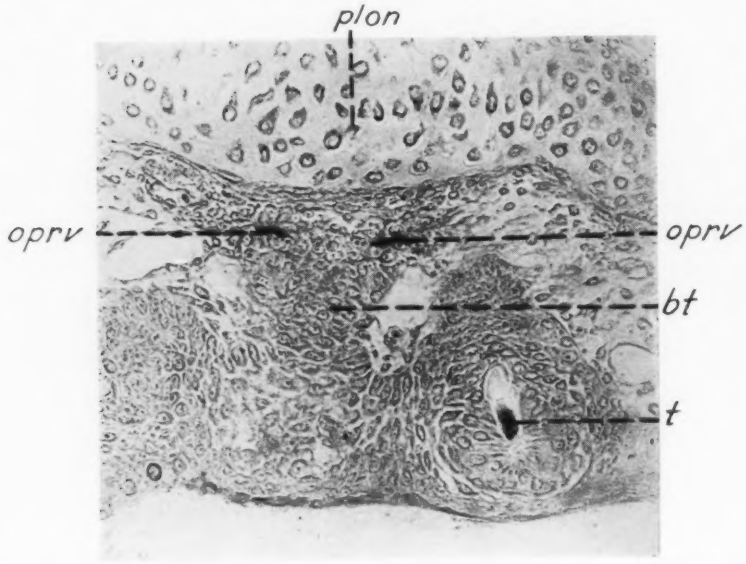

Fig. 43. Amia calva, 10.0 mm. Cross-section of anterior part of planum orbito-nasale showing blastematic primordium of prevomer with ossifications (*oprv*) in connection with basal part of a tooth rudiment (*bt*). Microphotograph.

of the development of these bones is certainly different. The origin of the bone primordium is the blastema formed in the place of the future bone. In this blastema the tooth primordium acts as an instigator, or as a centre of ossification in the blastema already formed. The bone itself thus has the same origin as, for instance, the maxillary or the pterygoids, the material it is built of is drawn from the same source, but its initiating ossification is provoked by the presence of teeth. As mentioned in the description of the development of the dental and the ectopterygoid, these two bones will be provided with teeth during their ontogeny, but, although there are points of teeth developed in the ectoderm even before the bones themselves are formed as primordia, there will be no connection between the primordia and the teeth until compara-

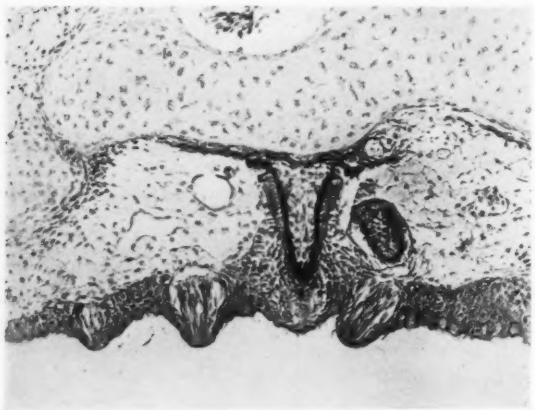

Fig. 44. Amia calva, 12 mm. Cross-section in the same position as in fig. 43 showing the tooth fused to the prevomer primordium. Microphotograph.

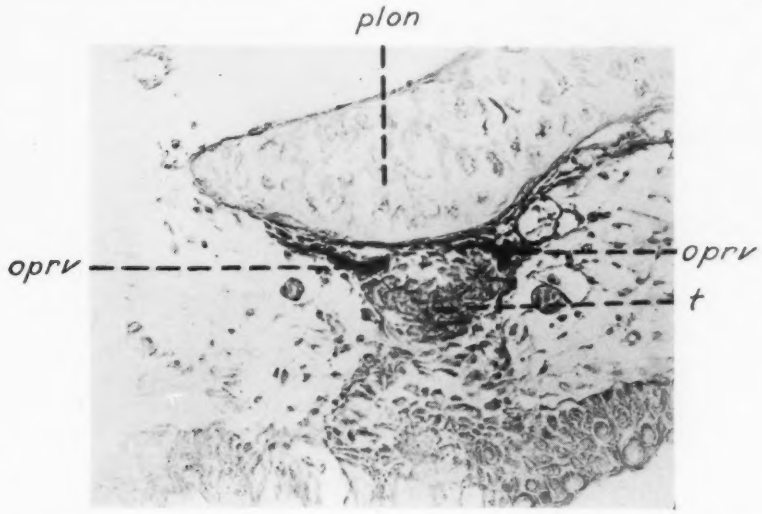

Fig. 45. Amia calva, 12.0 mm. Cross-section from the same stage but further back (cfr fig. 20). Letters as in fig. 43. Microphotograph.

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tively late. In the case of these bones, ossification of the teeth progresses from the point of the tooth towards the bone, where the tooth will eventually become fixed. This kind of connection between tooth and bone is no doubt to be considered as secondary, whereas the relations between teeth and bone is primary, as far as prevomer, etc. are concerned. Whether this primary connection between tooth and bone may be understood in OSCAR HERTWIG's sense or not, that is whether the bone has been derived originally from tooth bases or not, is a question that must be left unanswered. In any case it seems hardly possible to uphold it, at least not in recent fishes (MOY—THOMAS, 1937 a), although SÄVE—SÖDERBERGH (1933) takes it for granted in the case of Rhipistid Crossopterygians, whose ontogeny is not known.

Dermopalatina. Dermopalatinum I and II develop from the blastematic tissue that forms the anterior end of the palatoquadrate. In a 9.5 mm specimen the anterior end of this cartilage is still growing towards the ends of the trabecles. This growing part consists of a centre of prochondrial tissue surrounded by the blastema, or preblastema, already mentioned. This portion is connected rostrally with the part of the same kind of tissue that gradually changes into the maxillary blastema further caudad. As even the blastemas of the ecto- and entopterygoids have their origin from the blastema-like anterior part of the palato-quadrate, there are in all not less than five bones on each side that develop from the same source, although in two different ways. Both dermopalatina develop like the prevomer. Dermopalatinum I appears in a 10.4 mm specimen as an ossification beneath one tooth. The

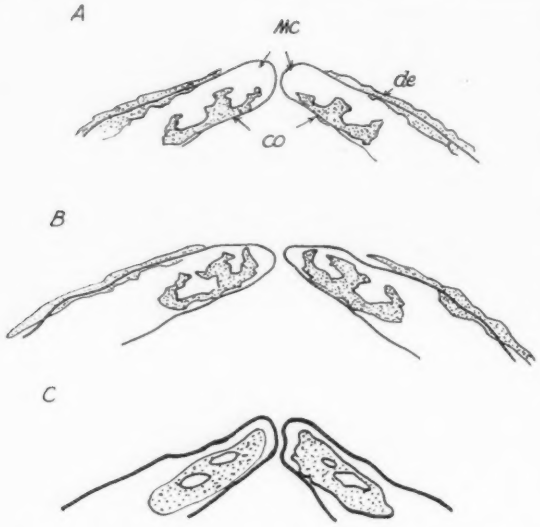

Fig. 46. Amia calva. Three stages in the development of coronoid I. Dorsal view of mandible, A of 9.5 mm specimen; B of 10.0 mm and C of 10.4 mm spec. (84 × 1.)

blastema that forms the matrix of the bone is situated on the ventral surface of the pterygo-palatine part of the palato-quadrate (fig. 39). In a 12 mm specimen yet another tooth base is added to the first from behind (fig. 29) and in a specimen measuring 13.8 mm (fig. 40) one more has joined the first two. From this primordium the bone grows in exactly the same way as the prevomer.

Dermopalatinum II forms considerably later. Not until the 20 mm stage is it seen as an ossification under one tooth base in a blastema situated laterally and ventrally near the end of the pterygo-palatine arch. It lies on a level with the caudal end of dermopalatinum I and the rostral end of the ectopterygoid.

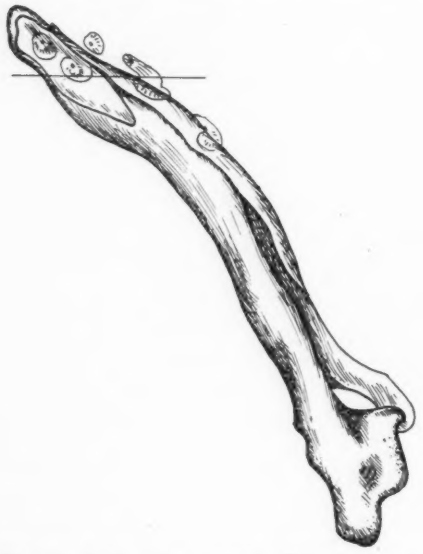

Fig. 47. Amia calva, 12 mm. Dorsal view of right mandible showing coronoid I with two teeth and dental with two teeth attached. Horizontal line, position of cross-section in fig. 48. (62 × 1.)

Coronoid elements. The coronoids in an adult Amia are two small tooth-bearing bones lying in front of the prearticular and covering the anterior end of the Meckelian cartilage from the inside. Exactly like the prevomer and the dermopalatina they develop under teeth. This blastema covers the inner side of the anterior end of the cartilage and belongs to the dental blastema. Coronoid I, situated most rostrally, develops very early. Already in a 9.5 mm specimen two ossifications on each side of the cartilage have fused to form the primordium of the bone (fig. 46). In a 10 mm specimen they are better developed and in a 10.4 mm specimen they are already filled

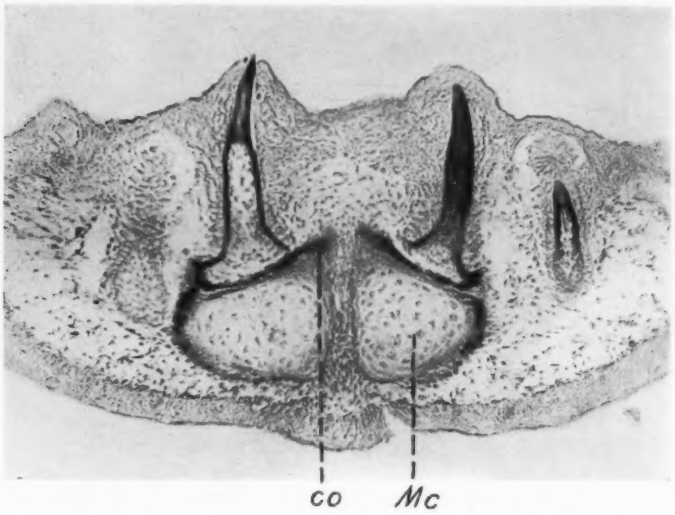

Fig. 48. Amia calva, 12 mm. Cross-section through anterior end of lower jaw (cfr fig. 47). Microphotograph.

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in with bone, and the coronoid has formed. In fig. 47 is seen a reconstruction of the right Meckelian cartilage in a 12 mm specimen, with the complete coronoid I carrying two teeth. To the right is the dorsal edge of the dental with three teeth. The microphotograph fig. 48 is a cross-section indicated in fig. 47 by the horizontal line.

Coronoid II develops in the same way. It forms as late as in a 21.5 mm specimen under one tooth behind coronoid I. In a 34.5 mm specimen the bone carries three teeth. In the same stage there is behind coronoid II another separate bone, forming in exactly the same way beneath one primary tooth base. But yet another bone of the same kind will eventually develop. In a 56 mm specimen the anterior end of the Meckelian cartilage is covered medially with a row of four coronoid bones. They reach from the tip of the mandible and backward to the anterior end of the prearticular. As the 56 mm specimen is the oldest one I have had the opportunity of examining, I have been unable to follow the change from the stage with four free coronoids to the adult stage with only two, but, judging from the size and position of the bones, I consider it most probable, that the second coronoid in the adult Amia is formed by the fusion of the three last coronoids of the young fish.

The great number of coronoids is typical of primitiv Actinopterygians.

Premaxillary. This bone develops in a slightly different way from the rest of the bones of the prevomer group. As was mentioned already in the description of the development of the prevomer, the anterior ends of the trabecles in a 9 mm specimen are surrounded by the usual more densely nucleated embryonic tissue, from which blastemas of various bones take their

Fig. 49. Amia calva 12 mm. Cross-section through anterior end of head. Cfr fig. 29. Microphotograph.

origin. This originally uniform and undivided tissue differentiates in two blastemas on each side. One is situated ventrally and will develop into the prevomer. The other blastema is situated anteriorly and slightly dorsally to the tip of the trabecle. This is the first rudiment of the premaxillary.

Ossification begins, however, in two different places in this blastema. At the anterior edge there are two tooth rudiments, one medial and one lateral. They form one centre of ossification in shape of the usual horseshoe-shaped bones, which grow in size, fill out and form a plate. But ossification takes place even in the dorsal part of the blastema, where a thin oblong disc of bone is formed spontaneously in the same way as for instance, the maxillary ossifies (fig. 49). As bone is formed in both places simultaneously, the result is, that the ossification under the teeth will be situated at the edge of the spontaneously formed part of the bone.

Three different stages of the formation of the premaxillary are shown in figs. 42, 29 and 40. In fig. 49 the anterior, dental part of the bone is clearly distinguishable from the posterior and dorsal part, situated above the cartilage.

As has been shown above, bones of the maxillary type ossify in a different way from bones of the prevomer type. The premaxillary forms in both ways, the anterior part in one way and the dorsal-caudal part in another. The reason might be that the bone, seemingly being one single unit, is originally derived from two different elements, one dental part and one ossifying spontaneously, which fuse during the course of development ontogenetically and

correspond to the tooth-bearing part of the bone in the adult fish and the facial part respectively.

Gular. The first rudiments of this bone appear in a 12.5 mm specimen (fig. 50 B), where five separate rudiments are to be seen. Ossification has begun only in the middle one, the others still being aggregations of osteoblasts. As the reconstruction shows, the rudiments arise in the vicinity of pit organs. Their material, as far as I have been able to see, is not derived from the sense organs, and they are, obviously, not even topographically bound to the sense organs, as closely as are the canal bones to the canal organs. One rudiment lies very near a pit organ, but not even there any close connection exists. In a slightly younger specimen, measuring 12 mm (fig. 50 A) the gular proved to be slightly more advanced. The rudiments—if four or five cannot be made out with certainty—have already fused on the right side. In a 13 mm specimen the separate rudiments have already fused and form a very irregular little bony plate, growing in all directions (fig. 50 C). As I am unable to find any fixed pattern in the development of the bone, I am inclined to consider the gular a bone of minor morphological value. In that respect it might be considered a bone of the type WESTOLL (1936) has named anamestic. Thus the gular—at least in Amia—although developing in close topographical relation to the gular line, does not depend on any sense organs for its origin, as the bones connected with the sensory canals of the head.

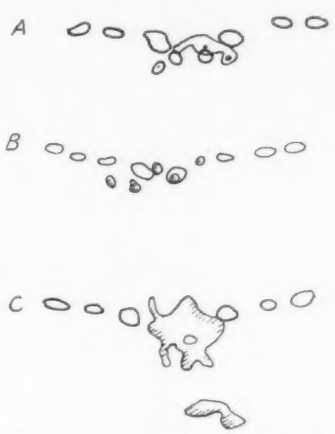

Fig. 50. Amia calva. Three different stages in the development of the gular bone. A, 12 mm specimen; B, 12.5 mm; C, 13 mm. (62 × 1.) Oblique lines, gular primordia; white circles, pit organs in the gular line.

KEY TO TEXT-FIGURES.

al. anterior head line of pits
ang. angular.
ant. antorbital.
angsp. angular-splenial.
chl. horizontal cheek line of pits.
co. coronoid I.
cod. coronoid teeth.
de. dental (-splenial).
dpal. dermopalatinum I.
dsph. dermosphenotic.
ectp. ectopterygoid.
entp. entopterygoid.
esc. extrascapular.
fr. frontal
hph. hypophysis.
it. intertemporal.
la. lacrimal.
Mc. Meckelian cartilage.
ml. middle head line of pits.
mpl. mandibular line of pits.
mx. maxillary.
na. nasal.
nch. notochord.
pa. parietal.
pl. posterior head line of pits.
plon. planum antorbitale.

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pmx. premaxillary.
po. postorbital.
pra. proc. ascend. parasphen.
pro. preopercular.
prvo. prevomer.
pq. palato-quadrate.
psph. parasphenoid.
ro. rostral.
scl. supracleithral.
so. suborbital.
spl. dental lateral splenial.
spm. dental medial splenial.
ssc. suprascapular.
st. supratemporal.
stco. supratemporal commissure organ.
stil. supratemporo-intertemporal.
t. tooth.
trb. trabecle.
vpl. vertical cheek line of pits.

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STUDIES ON THE HEAD IN FISHES

EMBRYOLOGICAL, MORPHOLOGICAL, AND PHYLOGENETICAL RESEARCHES

BY

NILS HOLMGREN

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1940

PART I:
DEVELOPMENT OF THE SKULL IN SHARKS AND RAYS.

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INTRODUCTION.

The present part of this work in 1931 was started upon my suggestion by GUNNAR KÄLLBERG, a pupil of mine. He intended to expand it into a thesis for the doctorate of science. His death in the summer 1933, however, stopped his work, but not before he had worked out a great number of beautiful reconstructions of developmental stages of the skull of *Squalus, Etmopterus, Scyllium, Raja, Torpedo* and *Urolophus*. He had also made a preliminary description of the different stages. Like most other workers on the development of the selachian skull KÄLLBERG had restricted himself to the study of the chondrified or chondrifying rudiments, paying no great attention to such mesenchymatic rudiments which do not become definite parts of the skull, but which, however, may be of great interest from comparative anatomical points of view. Nevertheless KÄLLBERG's research produced a number of interesting results well worth publishing, and, therefore after his death I undertook a preliminary revision of his reconstructions and manuscript to prepare them for publication. This revision made it clear that publication of the material as it then stood would be too precipitate, as there were errors to be corrected and gaps to be filled in. KÄLLBERG had paid very limited attention to the earliest rudiments of the head organs and incompletenesses especially with regard to the earlier stages of development were therefore inevitable. Since 1934 I have been occupied with redoing most of KÄLLBERG's reconstructions, filling in gaps and making new descriptions. Of KÄLLBERG's original reconstructions very little has been left unchanged, which does not mean, however, that there were not in his contributions many very interesting and important observations that will be duly acknowledged in this paper.

Every structure in a given stage of development is the result of an earlier ontogenetical process. It seems impossible therefore, to arrive at a deeper

understanding of the selachian skull without following its components as far back as possible. Since the skull is the result of the differentiation of the mesodermic tissues, its earliest developmental stages must be sought for in the early development and differentiation of the mesoderm (ecto- und ento-mesoderm). Only in this way can the principles of the formation of the skull be arrived at. Accordingly I undertook such a research on *Squalus acanthias* of which sufficient material was available. The general result of this research was stated to be valid for the other selachians as far as my material reached and I did not find it necessary to handle the earliest development of the other investigated species.

The investigations on the different sharks and rays have produced many results of comparative anatomical and phylogenetical interest. These I have recorded in the other parts of this work, where extensive researches on teleostomian fishes also have been made and where many points in their morphology have been elucidated in the ligth of the findings on selachians.

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To the present part of this work will only be added a few phylogenetical conclusions which have a somewhat important bearing on the next following part II.

The present part of this work will be succeded by the following parts:

Part II. On the comparative anatomy of the skull of recent selachians with remarks on the morphology of their dorsal fins (a phylogenetical study).

Part III. On the relations between selachians, acanthodians, arthrodires and holocephalians, and on the sensory line system of the head in fish.

Part IV. General morphology of the head in fish.

MATERIAL AND METHOD.

The material used in the first part of this paper consists of serial sections of embryos of the following sharkes and rays:

Squalus acanthias. Mostly transverse sections of the stages: 3.65, 4, 4.5, 5 (two series), 5.7, 6 (two series), 7, 7.8 (two series), 8 (two series), 9.2, 9.5, 10 (two series), 11 (two series), 11.25, 11.5, 12 (two series), 12.5, 13, 13.8, 14, 16 (two series), 16.5, 17 (two series), 18, 20 (three series), 21, 22 (two series), 22.5, 24, 24.5, 25.5, 26, 27, 30 (two series), 32 (two series), 33, 38, 39, 47, 48, 52, 59 and 84 mm bodylength (all measured after fixation).

Etmopterus spinax: Transverse sections of the stages: 11, 13, 15 (two series), 22.5, 24, 25, 27, 30, 34, 36, 43, 45, 47, 53 and 55 mm stages.

Scyllium canicula: Transverse sections of the stages: 2.5 (two series), 2.7, 3, 3.5, 5, 6.7, 9.5, 12, 13, 16 (two series), 18 (three series), 19, 20, 23.5 (two series), 27 (two series), 27.5, 30 (two series), 31, 32, 33, 38, 40, 55 and 90 mm.

Mustelus laevis: 25, 30 and 35 mm stages. Transverse sections.

Galeorhinus manazo: 23, 30, 41, 46 mm stages. Transverse sections.

Galeus zyopterus: 52 mm stage. Transverse sections.

Heptanchus cinereus: 75 mm stage. Transverse sections.

Heterodontus japonicus: 40, 43, 54, 58 and 62 mm stages. Transverse sections.

Chlamydoselachus anguineus: 127 mm stage. Transverse sections.

Raja clavata: Transverse sections of the following stages: 7, 7.5, 10, 11, 21.5, 36, 38 (two series), 40, 43, 46, 47, 50, 55 (two series), 58, 59, 60, 67, 79 and 90 mm.

Torpedo ocellata: Transverse sections: 4 (two series), 7, 7.5, 8, 11, 12, 12.5, 16, 17 (two series), 18 (four series), 20, 21, 21.5, 22 (three series), 22.5 23 (three series), 24, 24.5, 25, 31, 35, 41, 49, 63 and 71 mm.

Torpedo marmorata: 28 mm stage.

Torpedo sp. (probably *ocellata*): 11.5, 15, 16 (two series) and 17 mm.

Urolophus Halleri: 27, 31, 33, 49, 60 and 90 mm stages. Transverse sections.

For the other parts of this paper I have used a great number of sectional series of *Acipenser ruthenus, Gyldenstaedti* and *stellatus, Amia calva, Lepidosteus plathyrhynchus, Salmo salar* and *salvellinus* and a number of other teleostean fishes. To these are added some stray developmental stages of *Polypterus, Polyodon* and others.

The material mostly was fixed in Bouin's fluid. In some cases embryos fixed in Zenker's fluid and in formalin were used. The staining preferred for the reconstructions was the Azan-Mallory, and the pictures used by the reconstructions were photographical negatives.

The reconstruction method used was graphical. In ordre to get a good basis for the measurements the entire embryos were photographed or drawn before embedding in paraffin. Especially great care was taken to get the embryo placed with the sagittal plane perfectly horizontal so that a good outline could be obtained. This outline (the profil-line) then was used as basis for the reconstruction.

It is important to emphasite that the outlines of mesenchymatic condensations, blastemas and some prochondrial rudiments nearly always are impossible to draw in a quite objective way as they are more or less diffuse in the sections. Therefor two reconstructions from the same series of sections not always will be identical because the drawing of the outlines partly depends upon a personal equation. I believe, however, that the reconstructions mostly are reliable, as they have been tested at different occasions and from different points of view.

STUDIES ON THE HEAD IN FISHES

DEVELOPMENT OF THE SKULL IN SHARKS.

SQUALUS ACANTHIAS.

Since the fundamental work of SEWERTZOFF in 1899 the development of the skull of *Squalus* has been subjected to a number of investigations by SCAMMON (1911), VAN WIJHE (1922), MORI (1924) and HARRISON (1931). Nevertheless no detailed continuous description of this development has been made. The different workers have described their stages, but it has been difficult to get from the descriptions the sequence of the stages since the material investigated has been of different provenience and the development effectuates differently in different localities, as pointed out by VAN WIJHE in particular. SEWERTZOFF did not give any figures on the length of the stages reconstructed by him except that of the oldest which had a body length of 45—55 mm. VAN WIJHE's stages were 20, 22, 23, 28, 29.5, 30.5, 32.5 and 39.5 mm long. Of these he has figured the stages of 23, 28 and 39.5 mm. SCAMMON's stages were of 18, 20.6, 21, 24.7, 28, 34 and 37 mm. None was figured. MORI's stages (all figured) were of 44, 90 and 250 mm and HARRISON's of 10, 19, 25, 27, 35, 40 and 60 mm body length, of which the 25, 35, 40 (*Squalus Sucklii*) and 60 mm stages were figured.

KÄLLBERG tried to give a continuous description, based partly upon the descriptions of other authors partly upon his own investigations. In his figures the cartilaginous as well as procartilaginous rudiments were usually represented, whereas in those of other authors the cartilages only were usually demonstrated and he was therefore not able to give a continuous description.

The number of descriptions of developmental stages of *Squalus acanthias*, may be considered sufficiently great to allow a rather complete description of the cranial development of this fish, but the descriptions and reconstructions published by different authors are so inadequately made that it is quite impossible to compose from them a satisfactory developmental history of the skull. Actually the only reconstructions which could be used were those of SEWERTZOFF and VAN WIJHE; those af MORI and HARRISON being so incomplete or incorrect that it was necessary to reject them altogether whereas those of SCAMMON were without figures and too summary to be used. This being the case I found it necessary to make a description of my own, in which I could treat with the stages adequately, paying attention not only to the chondrified parts but also to the mesenchymatic rudiments of the skull. It was also necessary to increase the scope of KÄLLBERG's research to include the youngest stages, during which the blastemas of the different skeletal structures are forming. The investigations upon these stages produced so many points of view unknown to KÄLLBERG that very little of his original descriptions of the elder stages (38, 39, 47, 48, 59 mm) as well could be used.

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The appearance of every cranial component depends upon its earlier development and in order to come closer to an understanding of the cranial skeleton it is necessary to trace its development as far back as possible. This demand becomes more urgent if one strives to get dates for comparative anatomical and phylogenetical purposes. Surveying the literature on the development of the skull in selachians one undoubtedly gets the impression that the workers on this subject have to a too great extent begun their investigations with that stage where the *first cartilage* is developing, paying less attention to those very important developmental processes preceeding that stage. In reality the appearance of the first cartilages, the parachordals, is a rather late process in the development of the skull which in its blastematic or mesenchymatic stages has already received the outline which it retains throughout stages much later than the beginning of chondrification. When the description is restricted to the chondrified parts only, it is merely a description of the physiological process of chondrification in the already present membraneous or blastematic skull. Experience teaches (VAN WIJHE) that chondrification begins at very different stages in embryos of the same species from different localities, and my impression is that this variability in the appearance of cartilage also exists in individuals from the same locality. The development of the cartilages of the skull in *Scyllium* as described by DE BEER from VAN WIJHE-stained embryos gives the impression of a great individual variation in the appearance of the different cartilages and it is often very difficult to get the stages lined up in a continuous series with reference to the development of the different cartilaginous parts. This difficulty seems so great that a critical and detailed comparison between two close-lying stages of the same species may fail. If such is the case, it should be plain that a detailed comparison between the cartilaginous skulls of embryos belonging to different groups of selachians must be more or less hazardous.

In order to get a basis for these comparative anatomical considerations I have undertaken the following investigation on the development of the skull of *Squalus acanthias* for which a great deal of material was available.

Squalus acanthias, stage 3.75 mm.

In this stage the neuropore is closed but the brain has not been detached from the ectoderm frontally, a broad processus neuroporicus (fig. 1, *pr.ncur.*) still being present. The entodermal gut (*ent.*) extends frontally a conical process of entodermal cells, the premandibular mass (*pr. m.*) of DOHRN. This process ends at the caudal border of the processus neuroporicus. From the most anterior portions of the entodermal gut the notochord (*n. ch.*) is about to detach its anterior tip. The mandibular somite (*s.2.*) is also about to free itself from the gut and anterior (ventral) to this point the first rudiments of the premandibular somite (*s.1.*) and the "Platt's vesicle", "anterior

head vesicle" (*v.P.*) are forming. The mandibular somite, the premandibular somite and the Platt's vesicle form a series of outgrowths from the dorsolateral sides of the dorsal wall of the entodermal gut. I could not persuade myself that the two former represent somites, while the latter does not.

The trigeminal portion of the neural crest (*n.cr.2.*) is developing but its downwandering cells have still not attained the level of the notochord.

The only proliferating cells of the head somites are found dorsolaterally to the fore gut. They have proliferated from the mandibular somite and are angioblasts, the rudiments of the future carotid arteries.

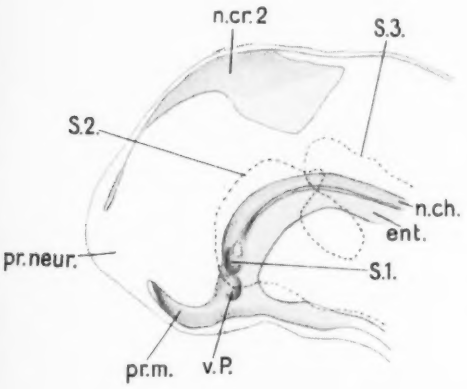

Fig. 1. *Squalus.* 3.75 mm. Neural crest and premandibular somit development. Reconstruction.

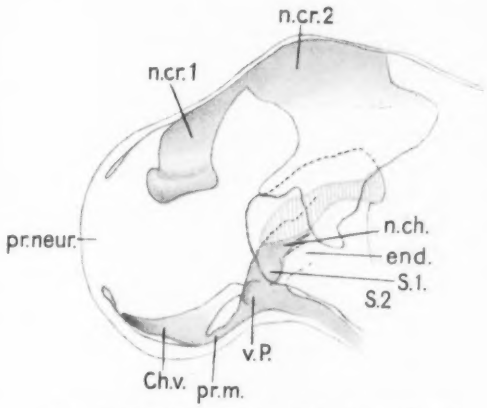

Fig. 2. *Squalus.* 4.6 mm. Neural crest and premandibular somit development. Reconstruction.

Squalus acanthias, stage 4.6 mm.

In this stage the mandibular somite (Fig. 2, *s.2.*) is quite detached from the preoral gut (Fig. 2, *end.*) and is already proliferating rather big cell-masses on its inside. This proliferation takes place chiefly from a frontal and a caudal centre, perhaps corresponding to the two sclerotomes of MATVEIEV. The "Platt's vesicle" (*v.P.*) and the premandibular somite (*s.1.*) are still in continuity with the entoderm and the tip of the notochord (*n.ch.*) is not yet detached. The premandibular mass of DOHRN (*pr. m.*) has differentiated and been divided into a posterior and an anterior portion (*Ch.v.*) (CHIARRUGI's vesicle), which, however, are still connected by a medial cell-string the cells of which are entering between the cells of the epithelium outside it. The anterior portion of the premandibular mass is developing laterad to embrace the brain ventrolaterally. From this widened portion of the "Chiarrugi-vesicle" a thin lamella of entomesodermal cells has grown caudad to meet the rudiment of the Platt's vesicle. In a 4 mm stage this lamella is also present but ends caudally a good distance anterior to the rudiment of Platt's vesicle.

The ectomesoderm developing from the trigeminal neural crest (*n.cr.2.*) portion has come down on the outside of the mandibular somite (*S.2.*) only. In addition a premandibular neural crest portion has arisen. From this portion a mass of ectomesodermal cells have attained the dorsal border of the eye-vesicle. Thus in this stage there could be no mingling of ectomesodermal and entomesodermal cells. In this condition my american embryos differ favourably from the mediterranean ones of DOHRN, where in 3.5 mm specimens the ectomesoderm has already attained the anterior portion of the premandibular mass, mixing with the cells of this mass.

Squalus acanthias, stage 5 mm.

The ectomesoderm has grown down over the sides of the head especially in the trigeminal region (Fig. 3, *n.cr.2.*). The ectomesodermal lamella lies, however, outside the big mandibular somite and therefore the ectomesoderm does not yet mingle with the entomesoderm which is already filling up the space inside the mandibular somite and extending dorsal to embrace the brain in the region of the brain flexure (*a.cr.*). The premandibular portion of the neural crest has given rise to a mass of ectomesodermal cells (*n.cr.1.*) bordering the eye vesicle dorsally and caudally. In this part of the head the ectomesodermal cell mass is well delimited from the entomesodermal.

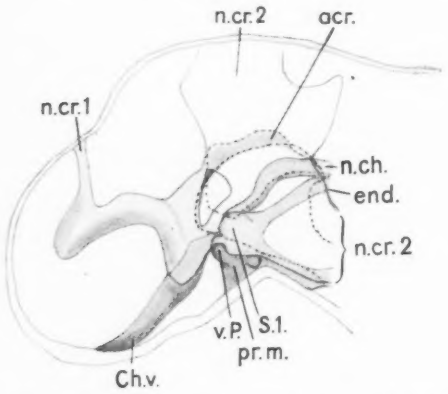

Fig. 3. *Squalus.* 5 mm. Neural crest and premandibular somit development. Reconstruction.

The entomesodermal elements of the preoral portion of the head consist of the as yet not detached rudiments of Platt's vesicle (*v.P.*), the premandibular somite (*s.1.*), and the remaining part of the tip of the posterior portion of the premandibular mass of DOHRN. The anterior portion (Chiarrugi's vesicle) (*Ch.v.*) is now completely separated from the posterior portion ventromedially. It frontally covers as a lamella of cells the midline portion of the brain ventrally and from this point on each side sends a lamella caudad to join the anterior tip of the PLATT's vesicle The only point where this entomesodermal lamella is in contact with the ectomesoderm is just in front of the vesicle, but here the ectomesoderm forms an external lamella of which the cells are easily distinguishable from those of the entomesodermal lamella. In front of the eye there is a considerable gap between the supraorbital ectomesoderm and the infraorbital entomesoderm.

Squalus acanthias, stage 5.7 mm.

In this stage development has advanced very much from the preceding. The ectomesoderm has grown down to cover the sides of the head outside the brain flexure and the prechordal somites. The trigeminal ganglion is developing from the neural crest material (fig. 4, *n.cr.2.*). The premandibular crest (*n.cr.1.*) portion has delivered ectomesodermal cells surrounding the eye frontally, dorsally and caudally. This big orbital cell mass is connected with the dorsal midline of the brain by the nervus thalamicus, which is the only nervous element arrising from this crest portion. Frontally the orbital mesenchyma forms a rather broad superficial area (fig. 4, *s.o.a.*). Below the eye the anterior premandibular mass (*ch.v.*) (CHIARRUGI's vesicle) completes the mesenchymatic ring around the eye. This ventral portion, however, is entomesodermal.

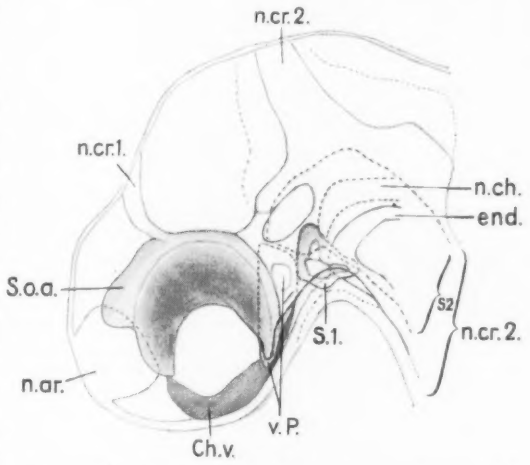

Fig. 4. *Squalus*. 5.7 mm. Neural crest and premandibular somit development. Reconstruction.

In front of the entodermal gut, the posterior premandibular mass has disappeared while the anterior end of the notochord has freed itself and the premandibular somite (*s.1.*) and the PLATT's vesicle (*v.P.*) have developed into independent structures. PLATT's vesicle lies directly in front of the premandibular somite. It is bigger than that somite and quite independent of it. It lies immediately behind the eye as an oblong cell body, the dorsal part of which is hollowed out into a vesicle. The ventral portion is solid, with radially arranged cells. At the tapering lower end of the body the cells are but loosely connected with the body as they are along the posterior margin of the solid part of the body also. These cells are apparently about to detatch from the vesicle.. The cell lamina of the anterior premandibular (*ch.v.*) mass is so intimately connected with the detached cellband that one could easily believe that the caudal part of this mass forms the cellband along the posterior border of the PLATT's vesicle. I am not able to answer this question. But whatever the answer may be, it is certain that this cellband is of entodermal origin and therefore also entomesodermal. There is, however, a slight possibility that some ectomesodermal cells may mix with those entomesodermal cells, but until this stage such a possibility is extremely problematic.

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Already in the 5 mm stage it is clearly seen that there are in addition to the neural crest other sources for formation of ectomesodermal cells, viz., the epithelium of the head in the trigeminal region and the epithelium of the mandibular arch. The latter especially is very important as very considerable masses of mesenchymatic celles are delivered from it to the arch. In the 5·7—7 mm stages this forming of ectomesodermal cells is very conspicuous.

Squalus acanthias, 7—8 mm stages.

The plica encephali ventralis is more pronounced than in the preceding stages. The premandibular somites are detached from the preoral gut conserving, however, their medial connection with each other by the premandibular commissure, lying closely anterior to the frontal end of the preoral gut. The premandibular somites form epithelial vesicles (fig. 5, *s.1.*). The vesicle of Platt lies as a long fingerlike body caudal to the eye vesicle. As in the preceding stages this vesicle caudally is bordered by a band of loosely arranged cells. Posteriorly the premandibular somite extends an evagination, into the upper (or anterior) part of the oral arch. This pouch for a short distance lies parallell with the muscular process of the mandibular somite (fig. 5, *s.2.m.pr.*). I should suggest it perhaps to represent the muscular process of a premandibular arch, as there is in later stages in front of the mandibular arch developed a rudimentary branchial pouch (VAN BEMELEN, 1886).

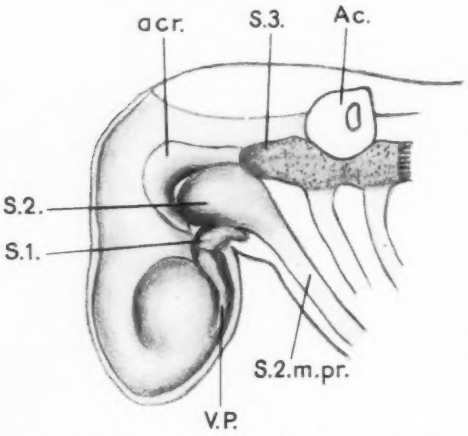

Fig. 5. *Squalus*. 7—8 mm. Head-somites. Reconstruction.

The mandibular somites have retired from the medial line and also shifted somewhat ventrad in relation to the encephalic flexure (figs. 8, 9, 10, 11, *s.2.*). They now lie as big vesicles near the ectodermal layer of the head sides. The tissue (*acr.*) lying between the two vesicles fills in the plica encephali ventralis perfectly. It is clearly understood from the sections and from the preceding stages that this tissue has proliferated from the medial wall of the vesicle, which seems to represent its sclerotome. There is no indication of two sclerotomes (MATVEIEV) in this stage. Simultanously it represents the acrochordal tissue. This mesenchymatic mass of cells at the encephalic flexure sends up short lamellae one on each side (fig. 5, 6, *acr.*), which embrace the lower part of the brain stem at this point. The muscular process of each

mandibular somite forms a wide tube entering the oral arch, ultimately joining the pericardium.

The development of the cephalic arterial system has caused the mesenchyma produced from the mandibular somites below the anterior part of the notochord and behind the hook of the notochord to be rather scattered. On the contrary the mesenchyma around the notochordal hook, in the bend of the brain stem and on the lateral sides of the anterior part of the notochord is very dense. Really the dorsomedial part of the mandibular somites has still preserved its activity of producing new entomesenchymatic cells.

The hyoid somite is a more or less cylindrical body, hollowed out in its anterior (figs. 11, 12, *s.3.*), solid in its posterior part (fig. 13, *l.bo.*). The sclerotome of this somite furnishes the material for the parachordals and for the lamina basiotica (its anterior part). The muscular process issues from the posterior half of the somite and enters the hyoid arch as a tube with a partly obliterated lumen (fig. 13, *s.3.m.pr.*). The basiotic lamina is formed from a solid part af the somite lying between the parachordal rudiment (medial sclerotome portion) and the muscular process (fig. 13), and corresponds to that part of the mesenchyma said by HARRISON (1931) to be the rudiment of the parachordal in a 10 mm stage of *Squalus acanthias*. Thus HARRISON's (1931) statement that the parachordals arise "below the otic vesicles and separated from the notochord by a distance equal to one half of its diametre in this region" is not correct. This description, however, corresponds very well to that of the basiotic lamina.

The first branchial somite is developed as the hyoid somite with a parachordal portion, a basiotic part and a muscular process to its branchial arch. The lamina basiotica thus consists of a lamina basiotica anterior and posterior respectively. The second branchial somite differs from the foregoing as there is a myotome belonging to it. The myotome part is developed in a portion of the somite corresponding perfectly to the basiotic laminas belonging to the first branchial and the hyoid somites respectively. The difference is that in the hyoid and first branchial somites also the myotome portion transforms into skeletal tissue.

The ganglionic crest material of this stage has lost its connection with the dorsal medial line except at two points, viz., in the region of the future epiphysis and at the future limit between mesencephalon and cerebellum (fig. 14). At the first mentioned of these points the feeble strand of the *nervus thalamicus* (fig. 14, 6, *n.th.*) connects the circumocular mesenchyma with the epiphysial region of the brain, and on the second point the *primary trochlear* nerve (fig. 14, 6, *pr.IV.*) forms a similar connection with the trigeminal ganglionic complex. As PLATT suggests, also I believe that the nervus thalamicus represents the sensory root of the N. oculomotorius and

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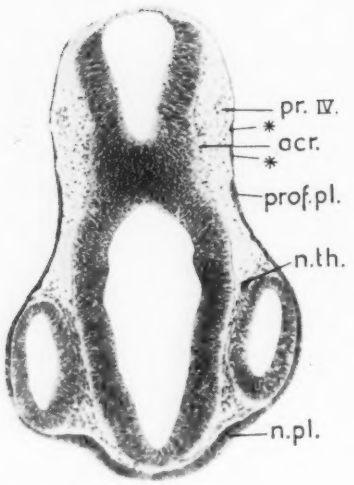

Fig. 6.

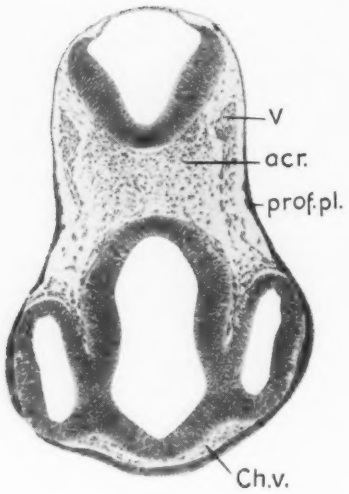

Fig. 7.

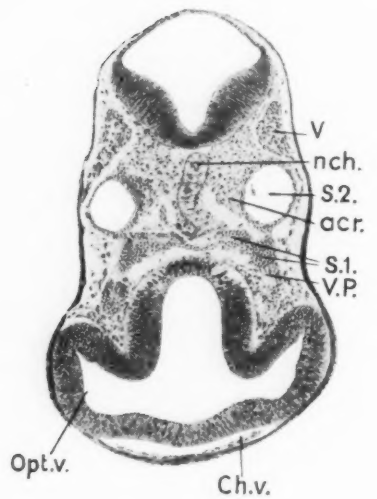

Fig. 8.

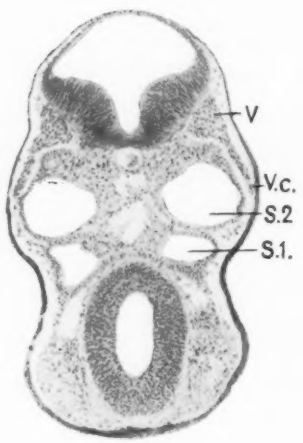

Fig. 9.

the primary trochlear nerve the sensory root of the future N. trochlearis. Both these sensory nerves soon disappear, as is well known.

The material originating from the anterior ganglionic crest is almost entirely ecto-mesodermic. In the actual stage it forms an incomplete mesenchymatic ring around the eye (fig. 14). This ring is superficial, lying close below the head-epithelium. It is developed frontal, dorsal and caudal to the eye. Ventrally it is substituted by the "anterior premandibular mass" (entodermal). Anteriorly the ring is broader than posteriorly and dorsally. The

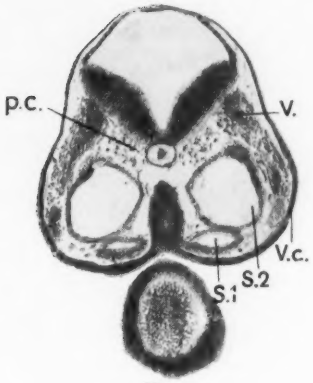

Fig. 10.

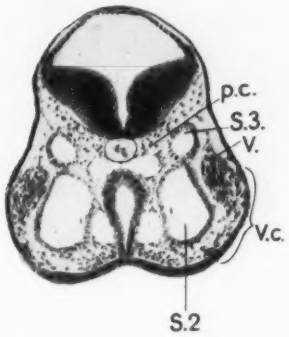

Fig. 11.

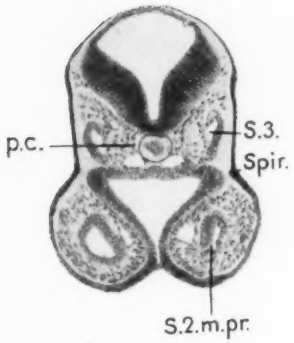

Fig. 12.

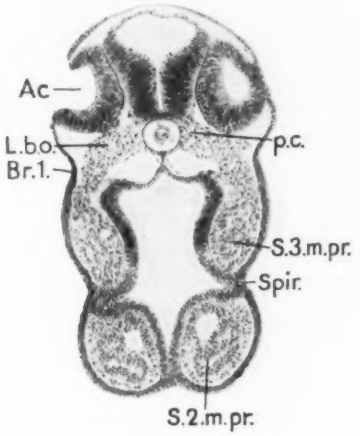

Fig. 13.

Figs. 6—13. *Squalus*. 7—8 mm. Transverse sections through the head region.

anterior broad part of the ectomesenchymatic ring extends toward the epiphysial region of the head. The ventral entodermal part of the circumorbital mesenchyma consists of a thin lamella on each side frontally joining the ventral border of the ectomesodermal circumorbital mesenchyma. It is caudally connected with the vesicle of PLATT. At this point it is overlayerd by a lamella belonging to the ectomesoderm and there a mixing of ecto- and entomesodermal cells could occur. The circumocular mesenchyma antero-ventrally contains a condensed portion lying inside a thickened part of the surface epithelium. This thickened part is the nasal placode (fig. 14, 6, *n.pl.*) and the condensed portion of the mesenchyma represents the rudiment of a *primary* nasal capsule.

The circumocular mesenchyma is thickest where it touches the epithelium. From there it sends out a lamella which covers the antero-mesial side of

the eye forming a combined primary sclerotica and orbital wall of the skull (figs. 14, 6, 7. 8). As the eye-tube of this stage is very wide, a big fenestra optica results in this "orbital wall".

The cell-material emigrated from the trigeminal ganglionic crest portion in the 7—8 mm stages has delivered the rudiment of the trigeminal ganglion complex (figs. 8—11, 14, *V.*), the primitive IV. nerve (figs. 6, 14, *pr.IV.*) and the main part of the mesenchyma of the oral arch. The trigeminal ganglion is in close contact with the skin on a wide surface (fig. 14, *V.ep.pl.*, figs. 9—11, *V.c.*) lateral to the pocket of Ratke at the brain flexure. This contact signifies an addition of ectodermal cells to the ganglion and is to be considered as an epibranchial placode. In this anterior (upper) part of the oral arch the ecto-mesoderm is in younger stages (7 mm) concentrated on the ventrolateral side of it, whereas in later stages (7—8 mm) the ecto-mesoderm anteriorly is concentrated medioventrally, and posteriorly surrounds the muscular rudiment entering the arch from the mandibular somite. This ecto-mesoderm of course, contains nervous system elements, but it is not possible from my sections to tell how much of them is present.

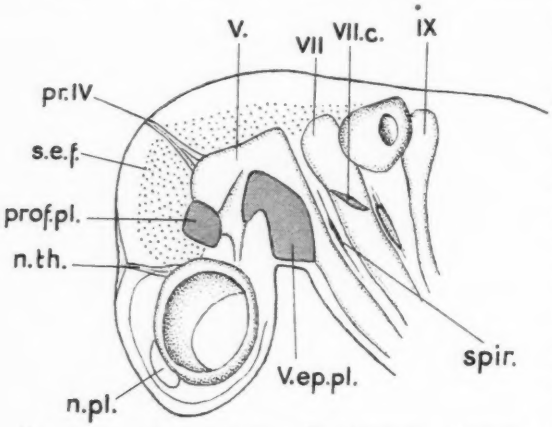

Fig. 14. *Squalus.* 7—8 mm. Development of neural crests and placodes. Reconstruction.

In the trigeminal part of the head the ectodermal placode of the profundus ganglion (figs. 14, 6, 7, *prof.pl.*) is present as a rounded disc of proliferation situated a good distance dorsal to the circumorbital ring of ecto-mesoderm. This placode still has no direct connection with the trigeminal.

Anterior to the profundus placode and the trigeminal a wide subectodermal field (fig. 14, *s.e.f.*) is occupied by scattered mesenchymatic cells. This field, already present in the 5 mm stage, does not reach the dorsal medial line of the head. These cells may be partly ecto-mesodermic, derived from the ganglionic crest, but the main part of them probably is derived from the ectoderm layer inside of which they are located. This layer is peculiar as it contains small medially directed projections in which a number of cells is crowded and from which cells are seen pushed inwards to become free ecto-mesodermic cells (fig. 6, *). This mode of formation of ecto-mesodermic cells is confined to the 5—8 mm stages. The field in question is not well

limited from the profundus placode, and could perhaps be considered as an extension of this placode.

Dorsal to the trigeminal ganglionic rudiment scattered cells are also present. These, however, seem to take their origin from the ganglionic crest.

Between the not yet opened spiracular gill-cleft, the acustic vesicle and the already opened hyoid branchial cleft lie the facialis ganglion and nerve rudiment and the mesenchyma of the hyoid arch (fig. 14, *VII.*), both products of the third ganglionic crest portion. The facialis ganglion has only a small epithelial contact (fig. 14, *VII.c.*) in front of the upper end of the hyoid branchial cleft. Between the spiracular and hyoid clefts and dorsal to this part as well as outside the otic capsule there are scattered ectomesodermic cells present.

Squalus acanthias, 7—12 mm stages.

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In 7, 7.8, 9.5 mm stages the vesicles of PLATT are connected ventrally by a thin lamella belonging to the anterior part of the premandibular mass of DOHRN. In 10, 11, 11.5 and 12 mm stages it is not possible to differentiate this lamella from the ecto-mesoderm which has grown down around the ventral surface of the head. From the 11 mm stage on, the vesicle becomes well delimited from the surrounding tissues. Compare the 12.5 mm stage!

Squalus acanthias, 12.5 mm stage.

In the 12.5 mm stage the spiracular canal as well as the two anterior branchial clefts have opened (fig. 15 a). The third to fifth clefts are present as grooves on the outside of the embryo. (These grooves correspond to entodermal pouches inside.)

The ectoderm of the head is thicker in its ventral and ventrolateral parts than in its dorsal, owing to the development of placodes or else thickened ectodermal parts.[1] Such an ectodermal thickening covers the frontal (that is the fronto-dorsal) surface of the head from approximately the anterior border of the fossa rhomboidalis to the anterior border of the nasal pit (fig. 15). This thickening contains two somewhat different parts, one dorsal (posterior) to the epiphysis, another ventral (anterior) to it. The latter seems already to be somewhat glandular in nature, and later becomes a glandular field (*g.f.*). A broad ring around the eye is covered by a thick ectodermal layer, which ventrally includes the nasal placode. The thickened circumocular ectoderm extends posteriorly over the branchial region, its dorsal boundary passing dorsal to the branchial openings and grooves. (fig. 15 a).

In this thickened ectoderm layer, or connected with it, a number of placodes is located, viz. the nasal, the profundus, the trigeminal with a lateralis com-

[1] The expansion of the brain apparently acts extending the dorsal parts of the head epithelium.

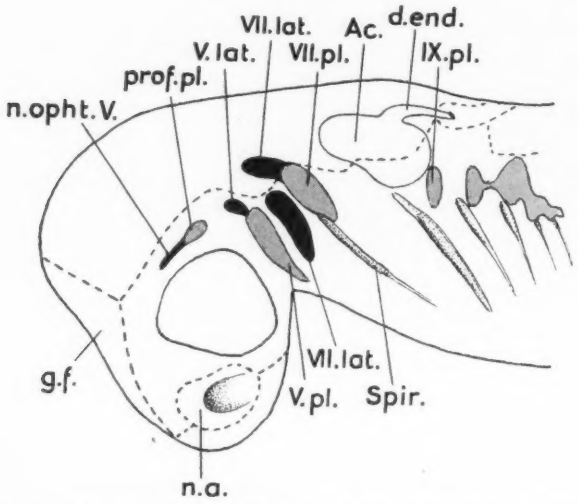

Fig. 15 a. *Squalus.* 12 mm. Epithelial fields and placodes. Reconstruction.

ponent, the facialis with its lateralis part, the glossopharyngeal and the vagus placodes (fig. 15 a). The otic placode forms the acustic vesicle (*Ac.*), which communicates with the exterior through the endolymphatic canal (fig. 15 a, *d.end.*). The aperture of this canal is surrounded by an ectodermal thickening extending caudad and mediad to connect with its vis à vis of the other side (fig. 15 a).

The nasal placode (figs. 16, 17, *n.pl.*) of this stage is invaginated forming a nasal vesicle with a wide external aperture (15 a, *n.a.*).

The profundus placode is found dorsal to the eye (morphologically dorsocaudal to it). The placode is oblong (figs. 15 a, b, 16, *prof.pl.*). Caudally it is connected with the rudiment of the profundus ganglion (fig. 15 b, *prof.ggl.*) and gives off cells to it; anteriorly the placode extends in an inwardly directed epithelial ridge formed by the basal parts of the ectodermal cell layer. This ridge marks the course of the future *nervus ophthalmicus superficialis trigemini* (fig. 15 a, *n.opht.V.*) and is the matrix of this nerve.

Behind the eye and ventrally extending to the anterior part of the oral arch the trigeminal ganglion is continuous with an oblong ectodermal area (figs. 15, 18, 19, *V.pl.*), the trigeminal (epibranchial) placode. A small lenseshaped ectodermal placode (fig. 15 a, *V.lat.*) is attached to its upper end. This placode gives rise to a rudimentary trigeminal sensory line portion with its primary nerve.

Behind the trigeminal area follows the facialis contact area (figs. 15 a, b, 20, *VII.pl.*). It lies at the upper end of the spiracular canal and connects the anterior part of the facialis ganglion with the ectoderm. Its upper end is continuous with a well developed ectodermal thickening (figs. 15 a, 18, 19,

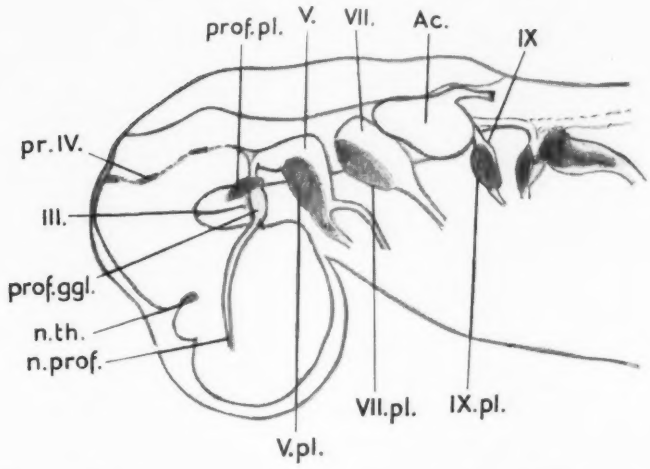

Fig. 15 b. *Squalus*. 12 mm. Cranial nerves and epibranchial placodes.

VII.lat.), lenseshaped in transverse section. This thickening represents the rudiment of the n. ophthalmicus superficialis facialis and the supraorbital line of sensory organs. The lower end of the contact area which extends into the dorsal wall of the spiracular canal, represents an epibranchial placode.

The glossopharyngeal contact area (epibranchial placode) lies behind the otic vesicle (figs. 15 a, b, *IX.pl.*). No lateralis portion is as yet discernible. The vagus ganglia also have contact areas of the same nature as the glossopharyngeal.

The head somites have not changed very much from the 7—8 mm stages. The premandibular somite (figs. 21, 17, 18, *S.I.*), however, is somewhat greater than before. Its posterior process (fig. 21, *s.I.p.*) is shorter. PLATT's vesicle (figs. 21, 17, *s.I.a., v.P.*) is as before, its upper end, however, lies lateral to the premandibular somite. There are still no signs of the premandibular somite producing mesenchymatic material. The vesicle of PLATT in 12.5 and 13 mm stages has changed, as it has got well defined boundaries. This condition has been brought about by the band of entomesodermal cells, bordering the vesicle caudally, which have been collected in a mesenchymatic strand along the posterior border of the vesicle. This strand is rather diffuse but in horisontal sections of 11 and 13 mm stages it is clearly determinable, and from these stages on it seems to be possible that this strand represents the first separate rudiment of the *trabecula cranii,* which thus in *Squalus* originally should be an entomesodermal structure, somitic of origin. But already in these young stages there are indications that also ectomesodermic material could enter the trabecular rudiment. But these are questions which need further investigations. The entomesoderm of the anterior premandibular

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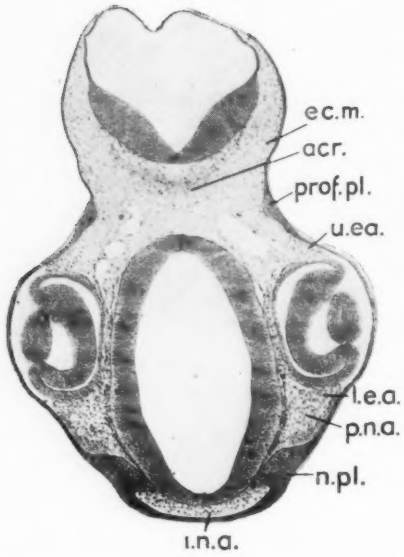

Fig. 16.

mass of DOHRN is not distinguishable any more as it has got mixed with ectomesoderm growing down from the circumocular ring to the ventral midline of the head. As the number of cells of the entomesoderm has been augmenting through the preceding stages it is not probable that this entomesodermal component of the head mesenchyma has become lost. The mandibular somite is as before (figs. 21, 17, 18, 19, *s.2.*), but seems to have largely decreased its function as producer of mesenchymatic cells for the acrochordal tissue. The hyoid somite (figs. 21, 18, 19, 20, *s.3.*) behaves as in the preceding stage. Anteriorly it is hollowed out, posteriorly it is solid. The vesicular portion (*s.3*) medially contains a sclerotome from which an anterior part of the parachordal forms. The other parts of the vesicle contain a myotome portion for the formation of the external rectus eye-muscle. The solid part from which the muscular process (fig. 21, *s.3.m.*) of the hyoid arch extends is located as a myotome but forms the anterior part of the basiotic lamina.

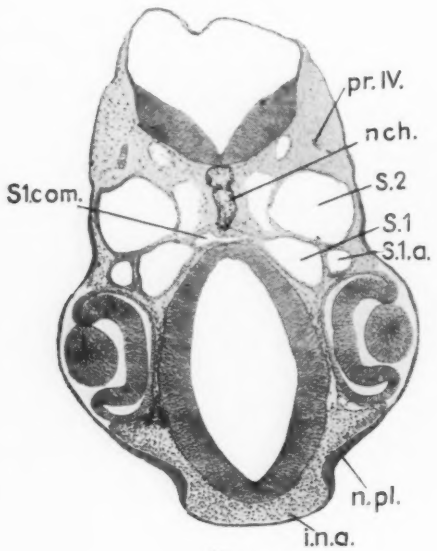

Fig. 17.

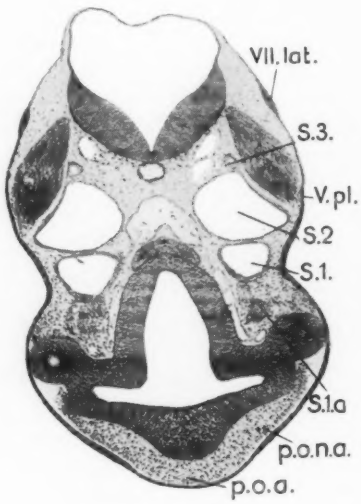

Fig. 18.

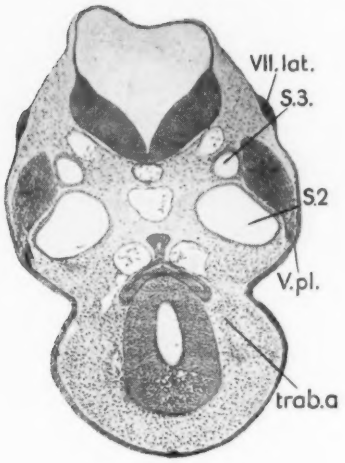

Fig. 19.

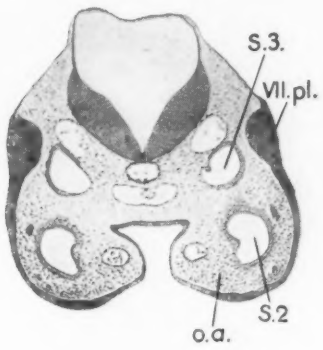

Fig. 20.

Figs. 16—20. *Squalus*. 12 mm. Transverse sections through the head region.

The first branchial or first metotic somite behaves as before, its "myotome" part developing to the posterior part of the basiotic lamina. In the second branchial somite the first real myotome is present in a position corresponding exactly to the basiotic laminas of the two preceding somites. (See reconstruction fig. 22.)

The ecto-mesoderm of the 12 mm stage fills the spaces between the organs of the head. At the brain flexure it is, however, not possible to draw up a limit between the somitic mesenchyma and that of the ecto-mesoderm (fig. 16, *acr.*). Nevertheless it is probable that the mesenchyma situated immediately below the skin epithelium in this part of the head belongs to the ecto-mesoderm (fig. 16, *ec.m.*), as do the other subepidermal mesenchymas. This mesenchyma does not form an uniform layer below the epithelium but is subdivided in fields of (somewhat) different aspect owing to different density of the cell arrangement.

Already in the 7—8 mm stages it is clearly seen that the circumocular mesenchyma is

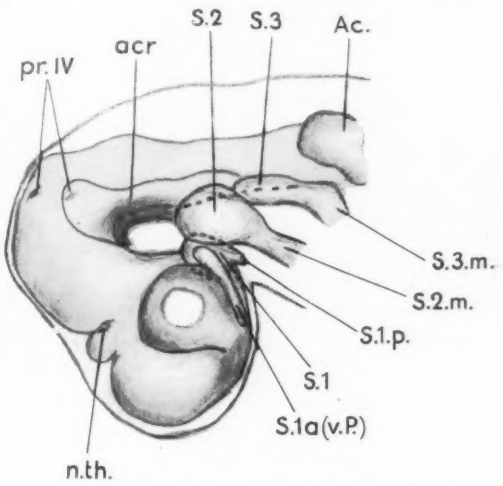

Fig. 21. *Squalus*. 12 mm. Head somites. Reconstruction.

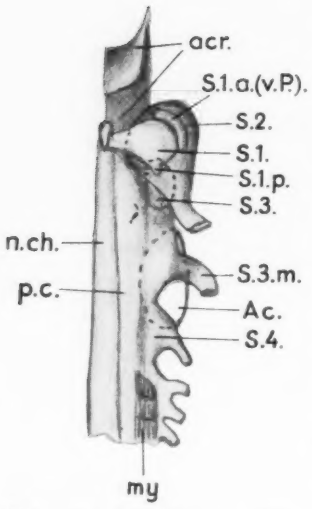

Fig. 22. *Squalus*. 12 mm. Entomesoderm. Reconstruction, ventral aspect.

continued dorsally by a thin mesenchymatic lamella extending toward the medial line of the head. In the 12.5 mm stage such a lamella has not only reached the mid-line but has also been differentiated from the remaining circumocular mesenchyma (fig. 23, *ci.a.*). Thus in front of the circumocular ring, viz., on the future dorsal side of the head, a field of rather scattered mesenchymatic cells forms a *frontal area* (fig. 23, *f.a.*) of considerable extension, embracing the rudiment of the epiphysis and frontally extending nearly to the rudiment of the nasal sac. Dorso-caudally it extends almost to the exit of the primary trochlear nerve. This mesenchymatic area in the midline has the same extension as the area of higher epithelial cells covering the frontal part of the head of the same developmental stage, but laterally its borders do not quite correspond to those of the epithelial area as is seen from the figures. The broadest part of the frontal area meets the broadest anterior (dorsal) part of the circumocular ring.

The circumocular mesenchyma or area anteriorly (dorsally) extends a broad triangular process (the epiphysial process) (fig. 23, *ep.pr.*) towards the broadest part of the frontal area. Ventrally (frontally) the circumocular ring is extended to form a big field, the ventral eye brow area, (fig. 16, *l.e.a.*) enclosing the nasal sac. This field is subdivided in an anterior *praenasal* (figs. 23, 16, *p.n.a.*), a *nasal* (fig. 23, *n.a.*) and a *postnasal area* (figs. 23, 18, *po.na.*). The praenasal (supranasal) area is continuous with the ocular ring and tapers posteriorly (inferiorly) into the nasal area. The praenasal mesenchyma is rather dense. Its superficial layers are arranged as an epithelium below the skin epithelium. The nasal area forms a bowl enclosing the nasal sac. This area represents a primary nasal capsule. The capsule flattens out posteriorly into the postnasal area which could scarcely be said to be well delimited from the ocular ring. The postnasal area follows the curvature of the ocular ring up to the cranial flexure. It contains in part the anterior premandibular mass (entomesoderm) mixed with ectomesoderm originating from the circumocular mesenchyme, which now, formes a closed ring around the eye, and seems to have sent lamellas ventrad to the ventral midline of the head. The ocular ring mesenchyma sends out a lamella inside the eye. This lamella forms a combined sclerotica and orbital wall. (fig. 23).

Between the two nasal mesenchymatic areas an *internasal area* (figs. 23, 16, 17, *i.n.a.*) is present, characterized by somewhat scattered medial cells and denser arranged lateral ones. Behind this area a broad and thick band

of scattered cells forms the mesenchymatic covering of the medial part of the head, the *preoral area* (fig. 23, 18, *p.o.a.*), anterior to the mouth opening. Caudally the preoral area meets with the ventral mesenchyma of the oral arch. The ventral part of the frontal, the internasal and the preoral areas form together the *medial area*. It is certain that the main part of this mesenchyma is derived from the premandibular neural crest, but it also contains ento-mesodermal elements and there is a slight possibility that part of it could have been derived from the mandibular neural crest portion ventrally joining the premandibular cell portion.

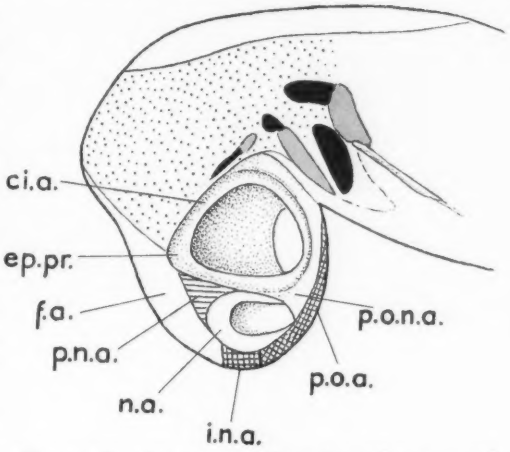

Fig. 23. *Squalus*. 12 mm. Mesenchymatic areas and placodes of the head. Reconstruction.

In the oral arch (fig. 20, *o.a.*) the mesenchyma is very dense on the ventral and ventromedial and on the lateral side of the arch. Almost the same arrangement was found in the branchial arches. The mesenchyma lying anterior to the spiracular canal and the branchial slits is arranged in small sphaerical clusters lying in an irregular row along the anterior border of the openings. This arrangement could scarcely be interpreted in another way than that these masses represent a set of rudimentary branchial or mesenchymatic rays. These structures, however, in the actual stage are still very indistinct.

The dorsal half of the head is covered by a mesenchyma composed of scattered cells.

Squalus, 16.5 mm stage.

The epithelium of the head of this stage as of the preceding is divided in epithelial fields, differing from each other through the different thickness of the epithelial layer. Except the placodes of the lateral line system which will be described later the following fields could be differentiated: 1. A frontal field (fig. 24, *f.f.*) of rather high, partly glandular epithelium which covers the frontal and dorsal surface i.e. that region of the head extending from the fossa rhomboidalis posteriorly to the nasal sac rudiment anteriorly. This epithelium, especially that anterior (ventral) to the epiphysial vesicle, forms a sort of gland or adhesive organ (fig. 25, *g.a.*). 2. Behind the dorsal part of the frontal field the epithelium covering the medulla oblongata dorsally is very thin (*occipital field*, fig. 24, *o.f.*). 3. Ventral to this thin part the epithelium

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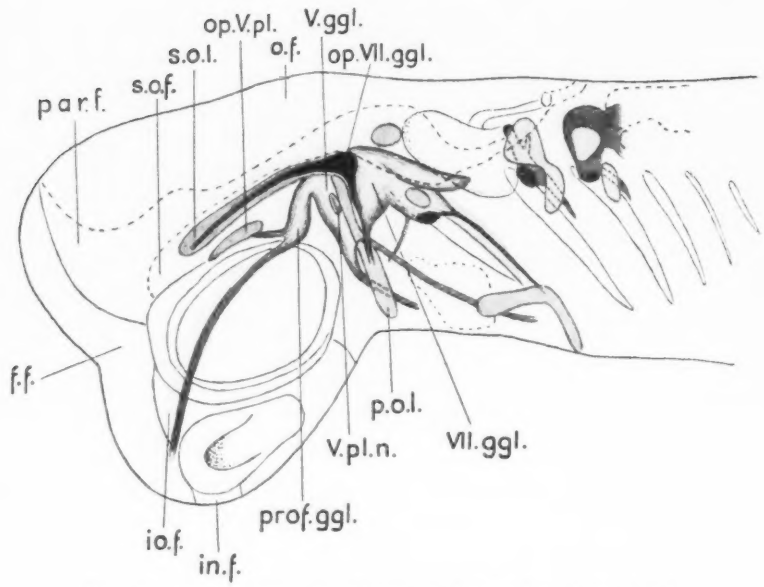

Fig. 24. *Squalus*. 16.5 mm. Nerves and placodes of the head.

becomes by degrees thicker above the eye, where the *supraorbital field* (fig. 24, *s.o.f.*) with the supraorbital line and the placode of the ophthalmicus superficialis has the thickest epithelium of this region of the head. 4. This field without limit extends over the branchial region forming 5. the *branchial field*. Frontally this field ends at the hind margin of the eye, which is covered by a rather high epithelium. 6. Frontally between the anterior end of the supraorbital line and the frontal field and dorsal to the supraorbital field the epithelium grows thinner by degrees. It is not, however, of uniform thickness but contains lenselike thickenings, suggestive of epithelial placodes. In the actual stage it was not possible to make an accurate reconstruction of these structures, but in the 22 mm stage we will come back to those formations. This field will be called the *parietal field* (fig. 24, *par.f.*). 7. Enclosed by the eye, the glandular part of the frontal field and the nasal placode there is a triangular field of slightly flattened cells. This field narrows posteriorly to a ribbon between the eye and the nasal placode. Posterior to the nasal placode it widens to cover the ventral surface of the head. This complex will be called the *infraorbital field* (fig. 24, *i.o.f.*). 8. Between the two nasal placodes the epithelium is thin, forming the *internasal field* (fig. 24, *i.n.f.*). The position and extension of these different fields is seen in the fig. 24.

In the 16.5 mm stage the lateral line system has attained a certain degree of development. The supraorbital head-line (figs. 24, 25, 28, *s.o.l.*), in the

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preceding stage present as a small rudiment, has now grown out as a rather long ectodermal thickening extending anteriorly towards the anterior portion of the eye. The ophthalmic nerve lies in the basal part of the epithelium. The anterior part of the ophthalmic ganglion has not yet been detached from the skin. Between the supraorbital line and the eye lies the placode of the n. ophtalmicus superficialis trigemini (figs. 24, 28, *op.V.pl.*). The posterior part of this nerve has separated from the epithelium, entering the profundus ganglion (fig. 24, *prof.ggl.*). The anterior part still lies in the thickened epithelium dorsal to the eye (supraorbital field). Caudal to the eye, at its upper-posterior margin, the small trigeminal placode (fig. 28, *V.pl.*) mentioned in the preceding stage has not developed very much, a short *nervc*, however, is about to form in the basal layer of the epithelium of this placode. This nerve enters the trigeminal ganglion (fig. 24, *V.pl.n.*).[1] Ventral to the mentioned placode, and in the same thickened epithelium as this, the postorbital part of the infraorbital line of sense organs is forming (figs. 24, 28, *p.o.l.*). The infraorbital part of the same line has not yet appeared. At the anterior end of the auditory vesicle a lense-shaped thickening of the external epithelium foreshadows a part (the otic?) of the lateral line (figs. 24, 28). As no nerve component, however, is yet developed, it is impossible to tell from the actual stage, what will become of this placode. At the posterior margin of the upper end of the spiracular gill cleft a small rudiment of the spiracular sensory organ is developed. This is innervated from the ramus oticus of the hyomandibular nerve. The latter also innervates a long band of thickened epithelium that borders the main part of the spiracular cleft posteriorly (figs. 24, 28). The same nerve also connects with the rudiment of

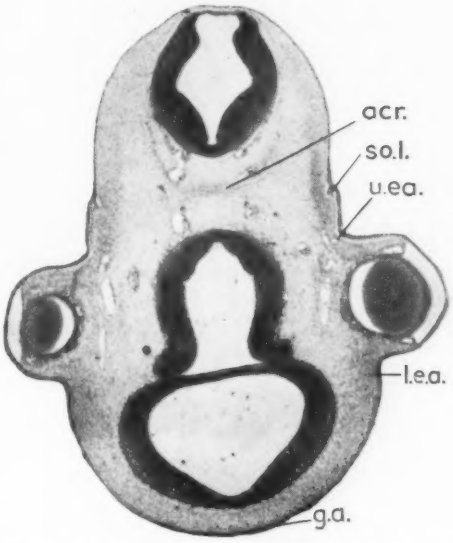

Fig. 25. *Squalus*. 16.5 mm. Transverse sections of the head.

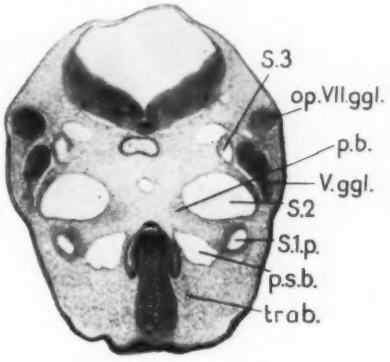

Fig. 26. *Squalus*. 16.5 mm. Transverse sections of the head.

[1] In the 22 mm stage this nerve has disappeared.

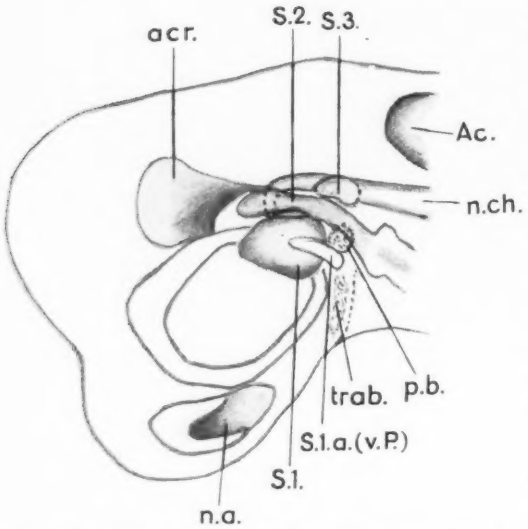

Fig. 27. *Squalus*. 16.5 mm. Entomesoderm (Head vesicles). Lateral aspect. Reconstruction.

the juguloangular line and the oral line of sensory organs (fig. 24). The hyomandibular ganglion has a connection with the epithelium somewhat above the middle of the spiracular cleft.

At the upper ends of the branchial clefts sensory line rudiments and ganglionic connections (*IX.* and *X.* nerves) with the epithelium of the clefts are present.

The head somites of this stage have changed in the following way.

1. The premandibular somite has grown greater. The PLATT's vesicle has decreased (fig. 27, *s.1.a.*). It now lies quite lateral to the premandibular somite. Its upper (posterior) end forms an oblong vesicle. Its lower end has fused with the lower portion of the lateral wall of the premandibular somite, and seems to take part in the formation of the obliquus inferior muscle. The same condition occurs in the 16 mm stage and also in the 17 mm stage, where, however, the upper part of the vesicle is solid. The mandibular process of the premandibular somite is somewhat bigger than before (fig. 26, *s.1.p.*).

2. The mandibular somite as seen from the lateral side is lower than in the preceding stage (figs. 27, 32, *s.2.*). Its anterior tubelike end extends frontad external to the profundus ganglion and close to the skin (rudiment of the obliquus superior muscle of the eye). At the level of the hooklike tip of the notochord the mandibular vesicle has its greatest transversal extension. Here its ventral and ventromedial wall is thinned owing to outwandering cell material which is forming a body of rather densely arranged mesenchymatic cells dorsal to the future pseudobranchial artery (fig. 26, *p.s.b.*), this body is still, however, not very clearly delimited from the adjoining mesenchyma and is the first appearing rudiment of the polar cartilage (fig. 27, 26, *p.b.*) of the trabecular system.—The mandibular vesicle is still connected with its muscular process, extending into the oral arch. The acrochordal (fig. 25, *acr.*) mesenchyma of this stage is very scattered and the only formed parts derived from it are that membrane of connective tissue forming a saddle-shaped part of the membranous brain capsule on which rests the ventral medial part

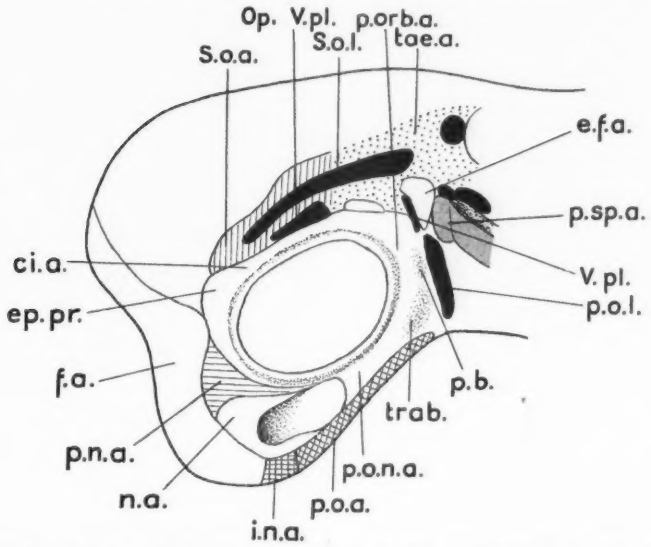

Fig. 28. *Squalus*. 16.5 mm. Mesenchymatic fields of the head. Lateral aspect. Reconstruction.

of the brain at the brainflexure (fig. 27, 25, *acr.*) as described in the preceding stage and a small but rather dense cell concentration behind the notochordal hook. VAN WIJHE, however, is of the opinion that the acrochordal condensation should develop from the commissure of the premandibular somites. "Das verdichtete Mesenchym der Kommissur setzt sich auch in den Chordahaken fort, dessen Krümmung ausfüllend und bildet von hier aus lateralwärts einen Flügel, der über den Augapfel hinzieht. In diesem Flügel, der sich ohne scharfe Grenze in das umgebende lockere Mesenchym verliert, entsteht nachher die Cartilago antotica, welche mit der Cart. supraorbitalis verschmelzend, den Pleurosphenoidknorpel bildet." According to my observations the premandibular commissure has nothing or very little to do with the formation of these structures.—The hyoid head vesicle has been greatly reduced (figs. 27, 26, *s.3.*) and its connection with its muscular process has disappeared. The posterior part of the hyoid somite has been used up partly in the formation of mesenchymatic parachordals and partly in forming the anterior part of the basiotic lamina as in the preceding stage.

The mesenchyma derived chiefly from the ganglionic crest, has augmented very much and, as in the preceeding stage, fills the spaces between the organs and the skin. The subepidermal mesenchyma of this stage forms areas as in the preceding. Thus a frontal, a circumocular, a prenasal, a nasal, an internasal and a postnasal and a preoral area are present (fig. 28). There is but one difference from the preceding stage worth mentioning, viz., that the most posterior part of the postnasal area has become differentiated from the

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rest. The postnasal areas posteriorly, lateral to the pocket of RATHKE, consist of densely arranged cells. These condensations are at least parts of the primary rudiments of the *trabeculae cranii* (figs. 27, 28, 26, *trab.*) and the area therefore could appropriately be called the *trabecular area.* The mesenchyma of the oral arch is still undifferentiated. There is no rudiment of the palatoquadrate distinguishable. The mesenchyma comes in contact with the rudiment of the trabecula frontally and could not be distinctly delimited from that rudiment, nor could it be separated from that mesenchyma covering the posterior lower surface of the preoral part of the head, which probably at least to a considerable part must have originated from the anterior (premandibular) neural crest portion. As the palatoquadrate later differentiates and the trabecula develops further, certain relations between the two structures, later to be described, arrise.

In this stage new areas have also appeared. The development of the rudiments of the lateral sensory system of the head seems to have been the stimulus for the development of an anterior supraorbital mesenchymatic condensation inside the supraorbital canal-rudiment. This mesenchymatic area, *the supraorbital area* (fig. 28, *s.o.a.*), is very clearly defined inside the anterior half of this canal rudiment. Inside the posterior half the cells become more scattered (*the taenia area* (fig. 28, *tae.a.*)), again to concentrate a distance anterior to the auditory vesicle to an *auditory capsule area,* where the area divides into a short superior and a long inferior branch embracing together the anterior end of the auditory vesicle. The postorbital part of the infraorbital sensory line is also accompanied by a mesenchymatic lamella, the *postorbital area* (fig. 28, *p.orb.a.*).—Anteroventral to the upper end of the spiracular cleft (fig. 28, *p. sp. a.*) and also along the anterior (ventral) border of the cleft a dense condensation of mesenchyma is present (*prespiracular area*).

Squalus, 22 mm stage (with remarks on the 17, 18, 20 and 21 mm stages).

The epithelial areas of the head have changed but slightly from the preceding stage, the changes chiefly depending upon the progressive development of the lateral line system which will be treated below. There appears, however, more conspicuously developed, a structure diffusely foreshadowed in the preceding stage, viz., a system of placodelike thickening in the epithelium between the parietal part of the frontal area and the supraorbital sensory field. In the 16.5 mm stage (and also in the 17, 18, and 20 mm stages) this parietal field is characterized by on transverse sections lenseshaped, bandlike epithelial thickenings. In these stages it was, not possible however, to discover any system in these structures. But in the actual 22 mm stage specimen it was possible to make a reconstruction of these thickenings. As seen from the figure 29 they form a system of three bands, issuing from the parietal field and abutting against the epiphysial process of the upper eye-brow-area. In

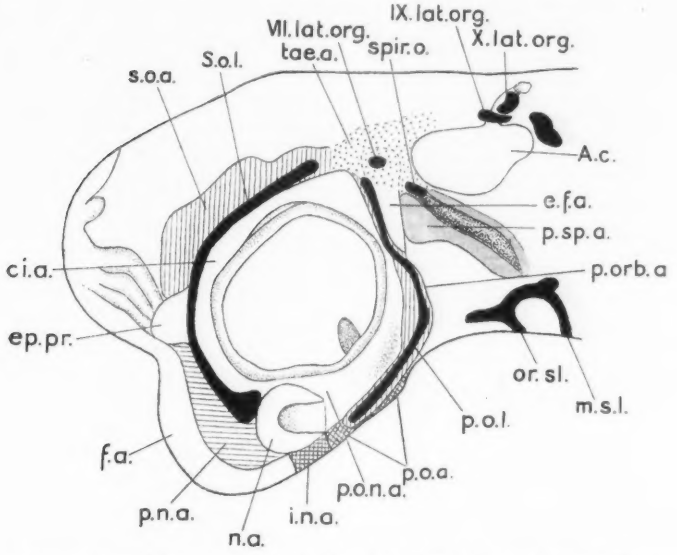

Fig. 29. *Squalus*. 22 mm. Mesenchymatic fields of the head. Lateral aspect. Reconstruction.

addition there is a short caudally directed thickening. These thickenings do not differ morphologically from thickenings initiating the development of lateral line placodes, but they do disappear and do not give rise to any definite structure. If they represent sensory line placodes, they must be considered rudimentary and perhaps of distant phylogenetical importance. It must be of interest therefore to make out their position in reference to the head of the adult fish. In the embryo they are paired, converging against a point situated between the epiphysis and the anterior border of the fossa rhomboidalis. In the adult head this point lies approximately in the centre of the dorsal surface of the head behind the eyes. It is, however, possible that these placode-like lines indicate a method for the growth of the skin

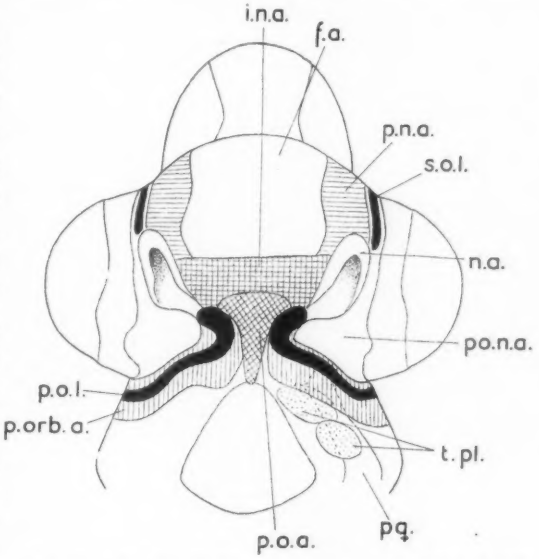

Fig. 30. *Squalus*. 22 mm. Mesenchymatic fields of the head. Ventral aspect. Reconstruction.

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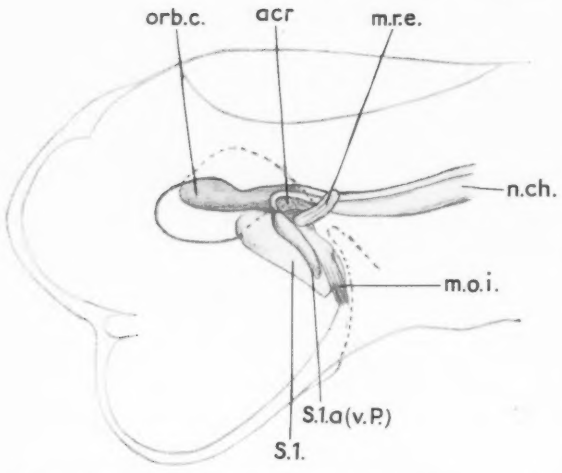

Fig. 31. *Squalus.* 22 mm. Entomesoderm (Head vesicles). Lateral aspect. Reconstruction.

covering the strongly growing brain of this stage and thus are centers producing the epithelial cells, necessary for the growth of the skin in this region.

The supraorbital sensory line of the 17 and 18 mm stages has not yet reached the anterior end of the eye. In the 20 mm stage its anterior tip lies in front of the eye and in the 22 mm stage it has bent round the eye anteriorly (figs. 29, 30), its tip now being about to enter between the eye and the nasal sac ventrally. The infraorbital line of the 22 mm stage extends from behind the eye down to the lower border of it and ends anteriorly closely behind the nasal sac (fig. 29, 30). The posterior ends of the supra- and infraorbital lines are widely separated (fig. 29). Two not yet innervated sensory line rudiments form the future horizontal posterior part of the infraorbital line. In a 22.5 mm stage they are innervated by the *VII.* nerve.

At the upper end of the spiracular cleft a sensory organ (Fig. 29, *spir.o.*) is developed and from it a band of thickened epithelium extends behind the cleft ventrally to join the rudiments of the sensory lines of the oral arch. These lines consist of the gular line and the oral line in the mandibular part of the oral arch (terminology of ALLIS). These two divisions of the oral arch system are dorsally connected with a longitudinal part, representing the angulo-jugal line of ALLIS.

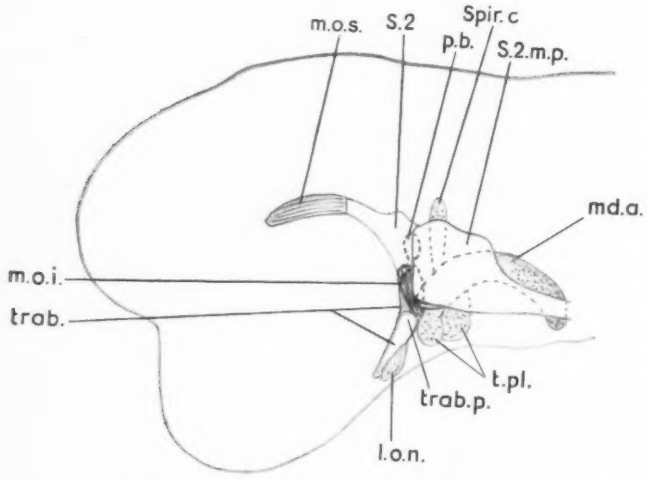

Fig. 32. *Squalus.* 22 mm. Entomesoderm (Head vesicles). Lateral aspect. Reconstruction.

Somewhat anterior to to the opening of the endolymphatic duct lie two

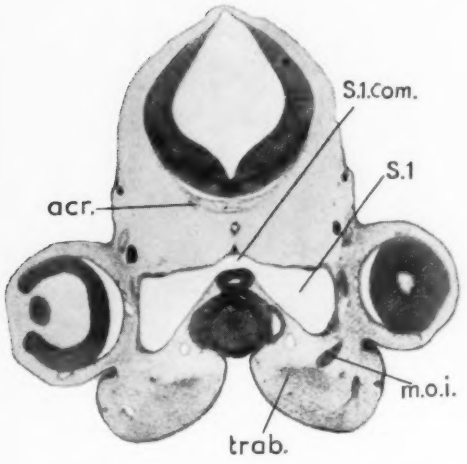

Fig. 33. *Squalus.* 20 mm. Transverse sections of the head region.

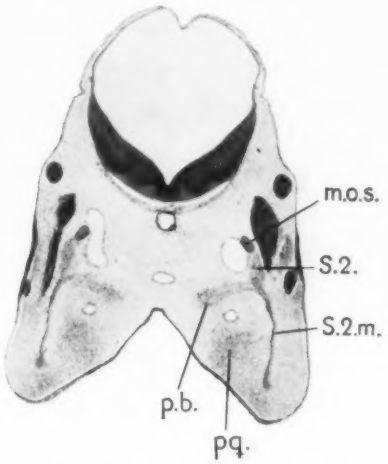

Fig. 34. *Squalus.* 20 mm. Transverse sections of the head region.

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sensory line rudiments, the anterior and ventral of which is innervated from the glossopharyngeal nerve (fig. 29, *IX.lat.org.*), the posterior and dorsal from the nervus vagus (fig. 29, *X.lat.org.*).

The nervus ophtalmicus superficialis *V.* placode has disappeared, the nerve now being separated from the epithelium.

In the 22 mm stage (as also in the 20 and 21 mm stages) the mandibular and hyoid somites have lost their lumina and their material is used for different purposes. The premandibular somite (fig. 31, *s.1.*) on each side always has a big cavitry, triangular in transsection (figs. 33, 35—37, *s.1.*), the two cavities communicating with each other by means of the premandibular commissure (fig. 33, *s.1.com.*). On the dorsal surface of the principal cavity insignificant rudiments of eyemuscles are present. The vesicle of PLATT has obliterated its lumen and transformed to a dense mesenchymatic rodlike structure lying closely to the mesenchyma of the eye-ball (fig. 31, 36, *s.1.a.*). Behind that point, where this rod extends from the somite, lies the rudiment of the obliquus inferior muscle of the eye (figs. 31, 32, 33, 37, 38, *m.o.i.*). In the 17 mm stage, as stated before, the upper part of PLATT's vesicle is solid and the lower part fused with the outside of the premandibular somite. This fused part is very thin. As it attains however, the ventral corner of the premandibular somite it widens to form a conical cell mass attached to this corner. In an 18 mm stage the lower portion of the vesicle has disappeared, but the premandibular somite seems to send down a distally solid process in a direction towards the trabecular rudiment, in the direction of the future obliquus inferior muscle and of the disappeared part of the vesicle. This process perfectly corresponds to the conical cell mass of the preceding stage. In a 20 mm

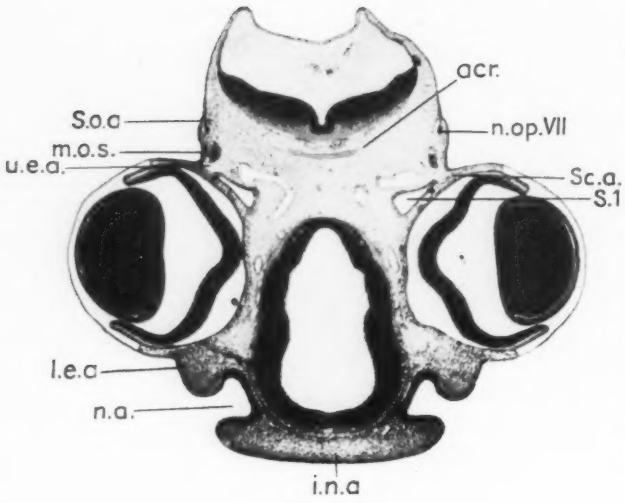

Fig. 35.

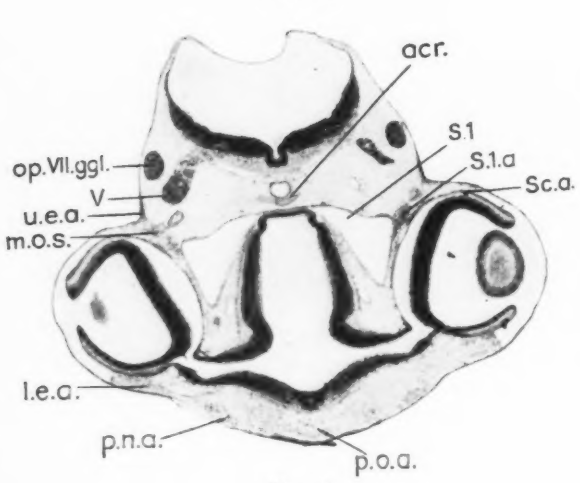

Fig. 36.

embryo the upper solid part of the vesicle of PLATT is joining the scleral tissue of the eye to form later the insertion surface of the obliquus inferior muscle (see later!). This muscle is developing and now it is clearly seen that it is connected with the wall of the premandibular somite as well as with the solid part of the vesicle of PLATT.

A carefull study of these conditions has convinced me *that the obliquus inferior muscle originates from the vesicle of* PLATT, *which also delivers the material for its insertion on the eye bulb.*

The mandibular somite has undergone great changes. Its anterior supraocular process has grown out considerably and its anterior portion has developed to become the rudiment of the obliquus superior muscle of the eye-ball (figs. 32, 34, 35, 36, *m.o.s.*). The rest of the mandibular vesicle with the exception of its muscular process has lost its lumen and been transformed into a rather dense triangular mass of mesenchymatic cells (fig. 32, 34, 37, 38, *s.z.*). The posterior portion of this mass is continuous with the rudiment of the polar cartilage (figs. 32, 34, 38, 39, *p.b.*), developed as describd in the preceding stage. Thus the polar cartilage of this stage has a big lateral appendix, which consists of a part of the degenerating (or transforming) remains of the somite (figs. 34, 38). The anterior part of the degenerated mandibular vesicle is continuous with the already mentioned anterior process. It has, however,

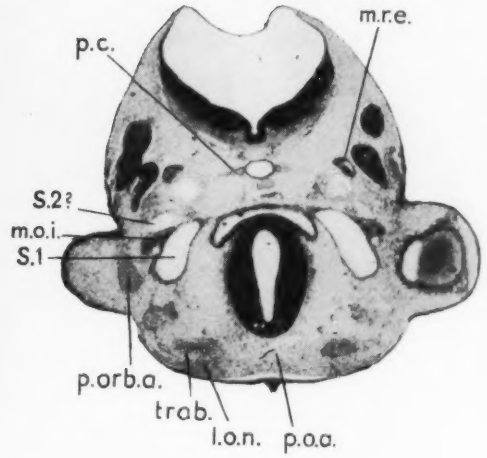

Fig. 37.

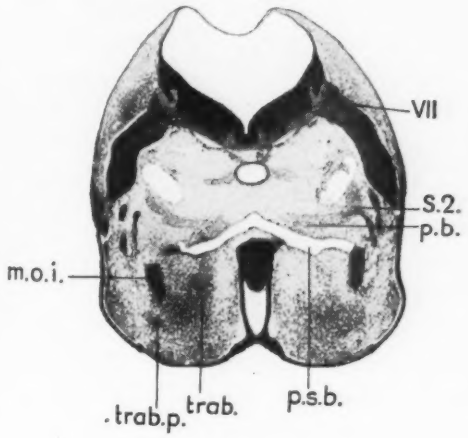

Fig. 38.

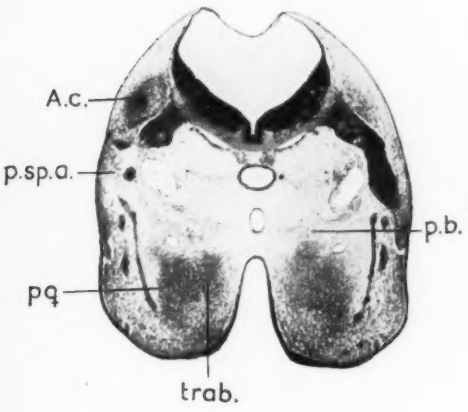

Fig. 39.

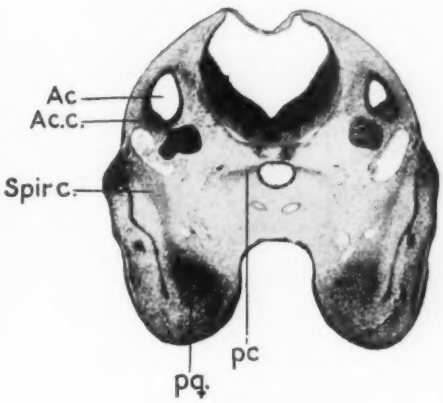

Fig. 40.

Figs. 35—40. *Squalus.* 22 mm. Transverse sections of the head region.

shifted frontad, associating with the dorsoposterior portion of the sclera of the eye, there forming a big body of connective tissue: the rudiment of the insertion part of the rectus externus and obliquus superior muscles. These transformations of the mandibular vesicle begin in the 18 mm stage where the upper and frontal inner surface of the wall of the mandibular vesicle becomes covered by a layer of collagenous fibres. With this layer the rudiment of the externus muscle lies in contact caudally and the posterior end of the obliquus muscle frontally. The rudiment of the polar cartilage ventromedially is connected with the wall of the vesicle. In the 20 mm stage the mandibular vesicle has lost its lumen transforming into a big body of connective tissue connected posteriorly with the rudiment of the rectus externus muscle,

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frontally with the obliquus superior, medially with the polar cartilage and ventrally with the muscular process of the somite. The connective tissue body in addition has shifted forwards towards the eye ball. From this description it is clear that I am not able to confirm DOHRN's statement, that the anterior portion of the rectus externus muscle in *Squalus* should be formed by the mandibular somite. In *Squalus* the externus muscle is quite a product of the hyoid somite, but the mandibular somite produces the connective tissue to which the muscle is fastened anteriorly.

The muscular process in the 22 mm stage is about to differentiate as muscle tissue. To the mandibular somite belongs that part of the acrochordal tissue, which is densely crowded inside the notochordal hook. This part of the tissue extends antero-laterally towards the supraorbital area (fig. 31, *orb.c.*) at the upper edge of the orbita forming the wings of the acrochordal tissue or cartilago antotica (VAN WIJHE). As previously, stated the lateral material of the acrochordal structure must be mixed up with ecto-mesodermal matter. Therefore it is not possible to define the limits between the somitic parts and the ecto-mesodermal parts of this region. For that reason it is possible that the extreme lateral part of the wing is ecto-mesodermal, whereas the most medial part is somitic in origin. The wing is laterally connected with the rudiment of the supraorbital cartilage, ecto-mesodermal in origin.

The hyoid head cavity has completely disappeared and the last remains of its walls have been transformed into the rudiment of the rectus externus muscle (fig. 31, 37, *m.r.e.*) of the eye.

The parachordals (fig. 37, *p.c.*, 38) of the 22 mm stage consist of a young prochondrium. They end anteriorly with acute angles lying close to the notochord.

The distribution of the ecto-mesodermal cells on subepidermal areas is much as in the preceding stage. Some very important differentiations and changes, however, have occured. The circumocular area has divided into a *sclerotic* (figs. 35, 36, *sc.a.*) and an (upper and lower) *eyebrow area* (figs. 29, 30, 44, 45). The sclerotic area is continuous with the mesenchyma, covering the eye on its inside, and is thus part of the primary eye-capsule or *sclerotic membrane*. The eyebrow area is enlarged anteriorly towards the epiphysial region of the head (fig. 29). Its dorsal part, the upper eyebrow-area, represents the first rudiment of the *supraorbital crest*. The supra-orbital area (*s.o.a.*) has shifted dorsad so that the supraorbital sensory line of the 22 mm stage borders the area ventrally with the exception of the posterior part of the line which always enters the area (fig. 29). At the anterior end of the supraorbital area the supraorbital sensory line enters the enlarged part the epiphysial process (fig. 29, *ep.pr.*), of the eyebrow area, pierces it and then continues on the boundary between the prenasal area and the infraorbital part of the eyebrow area (the lower eyebrow area) coming

to an end anterodorsal to the nasal sac. The supraorbital area contains the first rudiment of the orbital cartilage of later stages. As described earlier the rudiment of the cartilago antotica is directed against the supraorbital area with which it is connected. Undoubtedly the connecting cells are derived from the supraorbital area of which the deeper cells are scattered, forming a diffuse cellamina connecting with the lateral edge of the antotic rudiment. The upper (lateral) parts of the "pila antotica" thus probably contain cells, ecto-mesodermal in origin, whereas the ventral and medial parts are somitic. Probably there is a medium part of the pila which is of mixed origin. In the actual stage the outwandering of supraorbital cells is not sufficiently pronounced to produce a visible decrease in density of the supraorbital area. In later stages this is the case, and with regard to such stages (24.5 mm) it is possible to state that the outwandering cells, destined to form the main part of the supraorbital cartilage rudiment, have caused a visible thinning of the supraorbital area.

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The nasal sac is surrounded by a dense mesenchyma, forming the *primary nasal capsule* (fig. 35). The frontal, prenasal and internasal areas are much as before (fig. 29) but the postnasal area, which could not be well differentiated from the lower eyebrow area, has broadened and differentiated considerably owing to the development of the infraorbital sensory line (fig. 29, 30). In consequense of this broadening the preoral area has grown narrower (fig. 30), especially in its caudal parts. The differentiation of the postnasal area has already begun in the 16.5, 17 and 18 mm stages, but the results of this differentiation first become well visible in the 20 mm stage where the postnasal area is divided into an infraorbital and a *trabecular division*. The trabecular division in the 20 mm stage is developed in a certain relation to the infraorbital sensory line inside of which the mesenchyma now grows more densely, by degrees forming a dense mesenchymatic plate which curves along the anterior wall of the pocket of RATHKE and down at the postero-ventral surface of the head. The trabecular area is thus nearly perpendicular to the axis of the body. The said mesenchymatic plate contains the rudiment of the *trabecula cranii* (figs. 32, 33, 37—39, *trab.*). The development of the trabecula could be followed through the 18 and 20 mm stages to the 22 mm. In the 18 mm stage the primary trabecular rudiment lies as in younger stages, still closely to the posterolateral wall of the brain, but has organised an anterior (lower) lateral process, the future trabecular process. Immediately dorsal to this process is located the anterior tip of a somewhat condensed anterior portion of the mesenchyma of the oral arch. The origin of the trabecular process is obscure. It cannot be said that it is an outgrowth of the trabecular rudiment. It could as well have originated from cells added to the trabecular rudiment from the adjacent mesenchyma (of ectomesodermal origin). In the 20 mm stage the trabecular rudiment lies rather deep below the surface epi-

thelium and it is surrounded on all sides by a rather dense mesenchyma from which it has apparently got a considerable attribution of cell material; at least there are no signs of any augmenting of the trabecula from its own activity. A new mesenchymatic plate is forming outside the lower portion of the trabecular rudiment. This new plate becomes rather well defined in the 22 mm stage, where there is no difficulty in recognizing it as the mesenchymatic rudiment of the *orbitonasal plate* (fig. 32, 37, *l.o.n.*). Between the two trabecular areas of the 22 mm stage the unpaired preoral area (fig. 30, *p.o.a.*) has been compressed to a narrow field. The mesenchyma of this field is thick and reaches inside the surface of the brain case where it forms on each side a short lamella taking part in the formation of the primary brain capsule wall of this region of the head. The oblong cell-nuclei of this mesenchyma are chiefly arranged parallel with the ectodermal epithelium, transversal to the body axis. The above mentioned preoral area is that part of the medial area from which the keel on the basis cranii arises. Anteriorly, between the posterior parts of the nasal capsules, the preoral area broadens considerably, and its anterior limit simultanously becomes indistinct.

The eyebrow area is very narrow behind the eye, scarcely differentiated from the *postorbital sensory line area* (fig. 29). The latter area is ventrally continuous with the trabecular area. Behind the upper part of the postorbital sensory line area and flattened between the buccalis facialis ganglion and the skin epithelium lies a ventrally well delimited area af closely set mesenchymatic cells, the *extrafacialis area* (fig. 29, e.f.a.), already present in the 16.5 mm stage. Dorsally this area gradually gets poorer in cells and merges indefinitely with the posterior part of the supraorbital area (the taenia marginalis rudiment) where the latter area embraces the otic capsule rudiment. This point lies inside the anterior of the two sensory line organs (fig. 29, *VII.lat.org.*) later innervated from the otic branch of the facialis nerve. Rostral to the upper end of the spiracular cleft a well defined *prespiracular area* (figs. 29, 39, *p.sp.a.*) is present. Its cells are densely crowded. A strand of mesenchymatic cells, connected with the palatoquadrate rudiment and representing the rudiment of the *prespiracular cartilages* (fig. 32, 40, *spir.c.*), stops dorsally inside the upper end of this area. The prespiracular area is caudoventrally continued by a dense mesenchymatic band extending along the anterior border of the spiracular cleft. This band contains at the border of the spiracle rounded nests of mesenchymatic cells, apparently representing mesenchymatic matter of external gills or branchial rays not developing fully in that location.

In the mesenchyma of the oral arch the mandibular arch is differentiating as a thick rod of dense mesenchyma (figs. 32, 34, 39, 40, *md.a.*, *pq.*), bending round the mouth caudally. The anterior end of the rod is in continuity with the lateral process of the trabecula (fig. 38, *trab.p.*) on which is inserted

the obliquus inferior muscle of the eye (fig. 31). The trabecular mesenchyma and that of the palatoquadrate are in continuity with each other, and it is impossible to draw the limit between them properly. There is, however, a condensation for each, demonstrating where the future elements will develop. The relations of the palatoquadrate blastema and that of the trabecula will be described in the 24.5 mm stage. In the 16 mm stage the rudiment of the trabecula is present, whereas that of the palatoquadrate is not yet differentiated. As shown earlier the trabecular blastema probably is derived from the premandibular mass and from the first ganglionic crest, that of the palatoquadrate from the second. Its nearness to the palatoquadrate rudiment has caused the trabecula to be incorrectly interpreted as derived from the same rudiment (DE BEER). The rudiment of the mandibular arch is somewhat more advanced in its anterior palatoquadrate part than in its posterior, mandibular part, where it is still impossible to outline it properly. The palatoquadrate portion is connected with a subepithelial thick mass of mesenchymatic cells covering the ventromedial and ventral side of the oral arch respectively (fig. 34, 40). These cell masses are the rudiments of teeth complexes. A reconstruction of these rudiments shows that there are on each side of the palatoquadrate portion two such rudiments (figs. 30, 32 *t.pl.*), one anterior medioventral and a posterior ventral. These two rudiments may be called the teeth-plates. From them develop not only the teeth-pulps but also tissue connecting the teeth with the palatoquadrate and the palatine part of the palatoquadrate. The anterior end of the palatoquadrate proper represents the future orbital process region whereas the palatine process is still not differentiated from the teeth plates, which do not yet reach the medial line. The blastematic rudiment of the prespiracular cartilages has already been mentioned. It is connected with an anterior part of the mandibular arch (fig. 32, *spir.c.*).

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Squalus, 24.5 mm stage.

In principles the 24.5 mm stage has not changed from the 22 mm stage, in particulars many important differentiations have occured. The lateral sensory system has developed considerably. Thus the anterior tip of the supraorbital sensory line has penetrated between the eye and the nasal sac making a big ventral bend below the anterior edge of the eye (figs. 41, 42). The posterior end of the same line bends ventrad against the upper end of the postorbital part of the infraorbital sensory line. This line behind the eye now reaches the ventral surface of the head and extends almost to the medial line where it bends frontad in a right angle (fig. 42). This frontal part extends parallel with its partner of the other side past the posterior portion of the nasal sac. From the lower end of the postorbital part of the infraorbital line a caudal branch (the angular line (ALLIS)) is given off to the oral arch (fig. 41). The two rudiments of the *otic portion* of the infraorbital line have

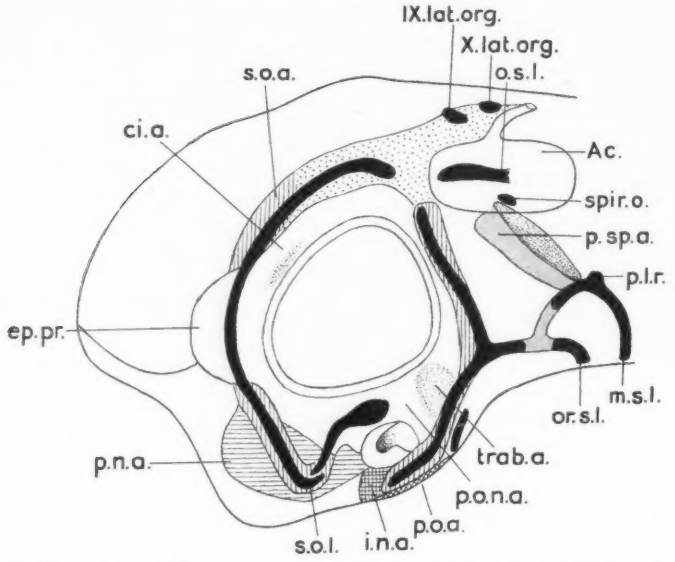

Fig. 41. *Squalus*. 24.5 mm. Mesenchymatic fields of the head. Lateral aspect. Reconstruction.

joined to an otic sensory line (fig. 41, *o.s.l.*) of which the anterior tip is directed towards the posterior end of the supraorbital canal. The glossopharyngeal and vagus sensory organs (fig. 41, *IX,lat.org., X.lat.org.*) of the head (pit lines) lie anterior to the orifice of the endolymphatic duct.

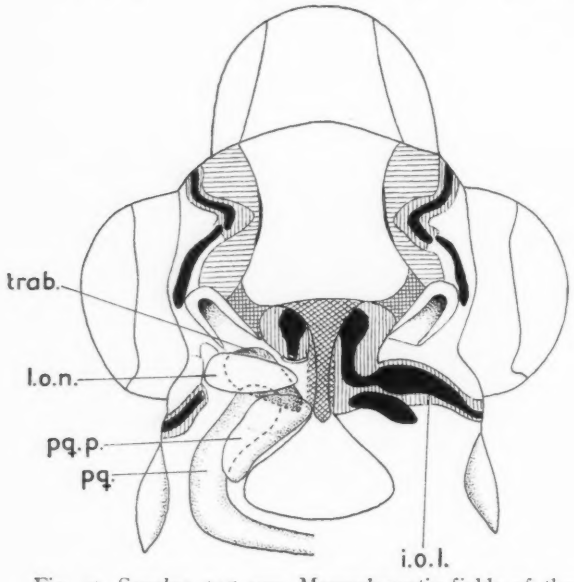

Fig. 42. *Squalus*. 24.5 mm. Mesenchymatic fields of the head. Ventral aspect. Reconstruction.

The premandibular head cavity is still present (figs. 43, 44, 47, 48, *s.1.*) but its relative size is considerably diminished as compared with that of the 22 mm stage. The premandibular commissure of the 24.5 mm stage is solid, its lumen being filled in with mesenchymatic cells derived from its walls. Anterior to the commissure the dorsal wall of the cavity has given origin to the rudiment of the

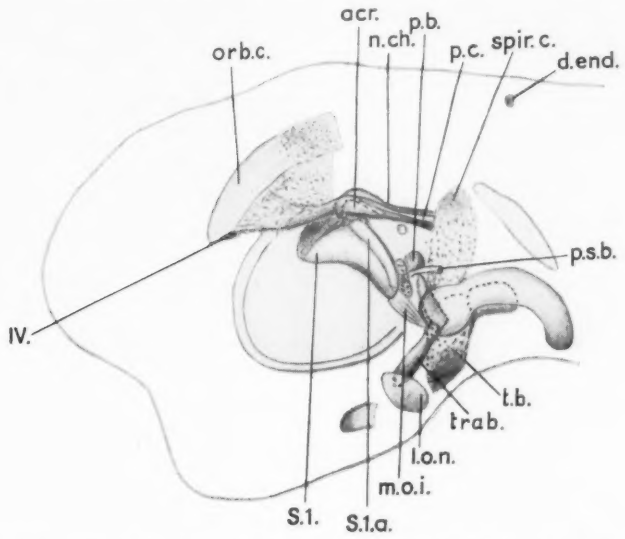

Fig. 43. *Squalus*. 24.5 mm. Head somites, trabecular complex, mandibular arch etc. Lateral aspect. Reconstruction.

rectus superior (fig. 44, *m.r.s.*) eye muscle and from the posterior part of the cavity its wall has given rise to the rectus inferior, and the rectus anterior muscle rudiments. The vesicle of PLATT[1] (figs. 43, 44, *s.1.a.*) is still present but as a dense oblong nucleus of mesenchymatic cells. This nucleus adheres to the primitive sclerotic membrane of the eye. The condensation appears ready to be transformed into prochondrium. The said nucleus is present in the 25.5 mm and the 27—28 mm stages but in the 30 mm stage it could no longer be discerned. In the 27—28 mm stages it has increased considerably and is incorporated with the sclerotic membrane, forming a part of its dorsocaudal portion internal to the insertion surface of the rectus externus muscle (and dorso-caudal and external to the point where the ophthalmic artery enters the eye bulb.)

The mandibular head cavity has disappeared. Cellmasses derived from its walls remain, however, as a considerable, irregularly shaped appendix (fig. 45, 49, 50, *s.2.*) connected with the lateral side of the polar cartilage (fig. 45, 49, 50, *p.b.*). Another formed part of the mandibular somite is that part of the acrochordal tissue forming a broad and long commissure (figs 44, 45, 46, 47, 48, *acr.1.*) between the rudiments of the orbital cartilages (figs. 45—47, *o.c.*, *orb.c.*) the proximal parts of which (antotic cartilage) are also derived from this somite, as explained earlier. That saddle-shaped membrane (fig. 44, 46, *acr.2.*) covering the ventral part of the brain at the great brain flexure

[1] For the relations of the vesicle of PLATT to the obliquus inferior muscle, see the preceding stage.

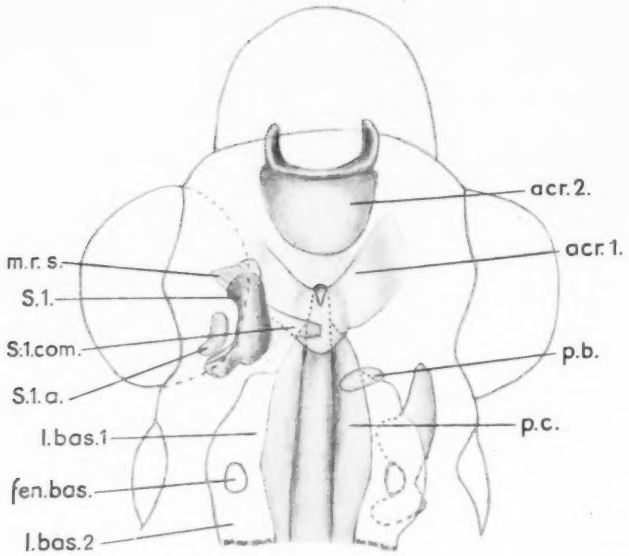

Fig. 44. *Squalus*. 24.5 mm. Entomesoderm of the head. Ventral aspect. Reconstruction.

which was described in preceding stages is also present. The rudiment of the polar cartilage (figs. 43—45, 49, 50, *p.b.*), derived from the mandibular somite as explained in the preceding stage, has condensed to a rather well defined body of young prochondrial matter, laterally carrying the appendix of mesenchymatic mandibular somite matter already mentioned. The rudiment of the obliquus superior muscle (fig. 46, *m.o.s.*), derived from the mandibular somite, extends frontally toward the anterior border of the eye where it ends in a condensation of the circumocular mesenchymatic area. The muscular plate of the mandibular arch now contains fairly well developed muscular fibres. The plate anteriorly covers the side of the head (fig. 51, *s.z.m*) behind the eye from the level of the anterior tip of the palatoquadrate to the lower part of the auditory capsule, but caudally it immediately narrows considerably.

The hyoid head cavity has disappeared and the material of the hyoid somite is distributed as in the preceding stage, forming the most anterior part of the parachordals (figs. 43—45, 48—51, *p.c.*), the anterior part of the lamina basiotica (fig. 44, *l.bas.1.*), the rectus externus muscle and the musculature of the hyoid arch.

The differentiation of the ecto-mesodermal cell material has progressed considerably from the previous stage of development. The posterior half of the supraorbital mesenchymatic area (fig. 41, *s.o.a.*) has become less distinct, depending upon the outwandering of its cells for the purpose of building up the rudiment of the orbital cartilage (spheno-lateral cartilage). Anteriorly,

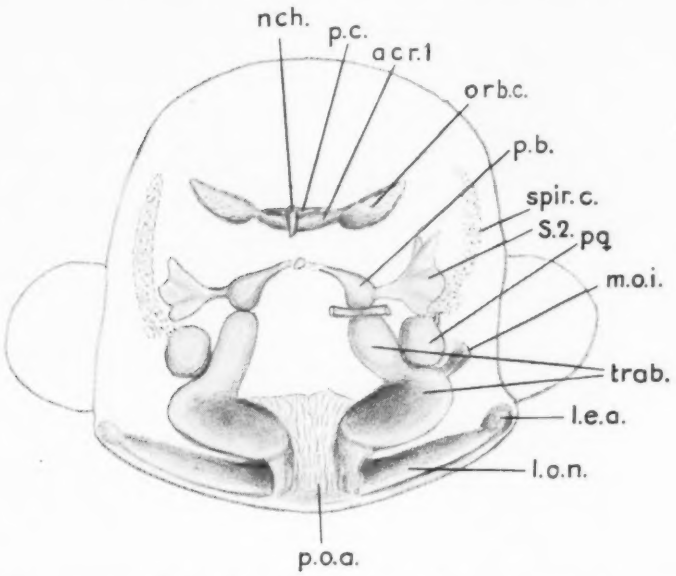

Fig. 45. *Squalus.* 24.5 mm. Trabecular complex from in front. Diagrammatic reconstruction from a few transverse sections.

where the supraorbital field has not yet begun such a function, its mesenchyma is still dense forming, together with that of the epiphysial process of the eyebrow area, an anterior part of the orbital cartilage rudiment. The infraorbital part of the eyebrow area has undergone great changes which are related to the big bend of the supraorbital sensory line below the anterior part of the eye (fig. 41). There the area has broadened considerably and its cells form a thick mass between the eye and the line (fig. 41, *s.o.l.*). In addition the mesenchyma has been differentiated in a band of cells inside the sensory line.

The anterior ends of the infraorbital sensory-lines have grown frontad and entered between the nasal apertures (fig. 42, *i.o.l.*). The internasal area has thereby been incorporated with the anterior part of the preoral area (fig. 42) which has thus become longer than in the preceding stage, and now includes the internasal septum. The trabecula (fig. 54, *trab.*) of the stage consists of a posterior, vertically located part ending ventrally (frontally) with the lateral trabecular process, with the insertion of the obliquus inferior (fig. 54, *m.o.i.*) muscle, and the connection with the palatoquadrate (figs. 54, 61, *pq.*), and an anterior nearly horizontal spoonlike portion. Whereas it seems possible that the posterior portion includes entomesodermic elements, as suggested before, the anterior portion seems to be formed exclusively by ectomesodermic cells delaminated and absorbed from the trabecular area (figs. 54, 59—62, *trab.*). Between the horizontal parts of the trabeculae the

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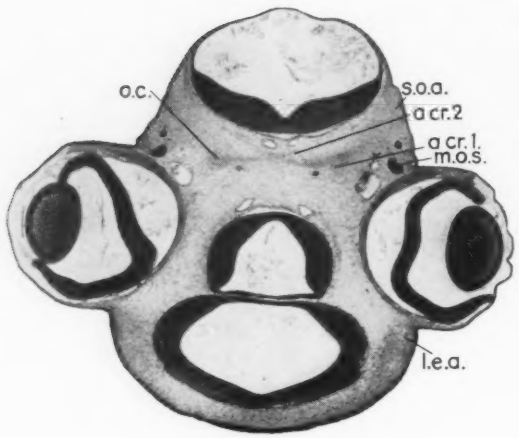

Fig. 46.

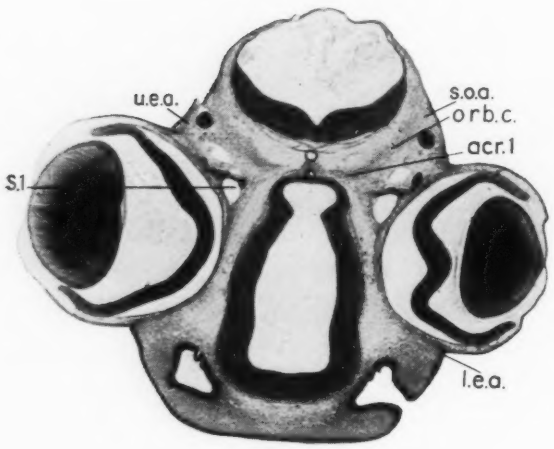

Fig. 47.

preoral area (figs. 54, *p.o.a.*, 60, 61) is compressed forming a mesenchymatic trabecular commissure. Outside the frontal part of the trabecula the orbitonasal plate (figs. 45, 48, 49, *l.o.n.*) is about to sink from its subepithelial position. In the infraorbital division of the postnasal area a thick mass of mesenchymatic cells (figs. 45, 48, 49, 50, *c.e.a.*) borders the lamina orbitonasalis laterally. In the 25.5 and 27 mm stages it is clearly seen how the orbitonasal lamina gets into close relation to the trabecula. The middle portion of the lamina is bent upwards so that it comes in contact with the lateral process of the trabecula immediately anterior to the point of origin of the obliquus inferior muscle. The lateral part of the orbitonasal lamina is thus bent down. The medial part is more or less intimately fused with the ventral surface of the trabecular "spoon".

The postorbital sensory line area of the 24.5 mm stage has broadened considerably dorsally, as the extrafacial area has fused to it (fig. 41).

The mandibular arch is still mesenchymatic, but its palatoquadrate portion is perhaps about to be transformed into a young procartilage. From the anterior end of the arch a blastema (fig. 42, *pq.p.*) extends mediad towards the posterior portion of the preoral area of which a part thus becomes enclosed between the tip of this blastema and that of the opposite side. This blastema contains the rudiment of the palatine process of the palatoquadrate together with the blastema of the teeth plates. The process forms *in situ* and

does not grow out from the palatoquadrate. The tooth blastema of the palatoquadrate consists of two plates, an anterior on the palatine part and a posterior on it and on the palatoquadrate proper. On the mandibular portion only one such plate is present on each side.

The relations between the trabecula and the palatoquadrate are the following. As already mentioned the anterior tip of the palatoquadrate rests upon a process on the lateral side of the trabecula. Here the ventral surface of the palatoquadrate tip is in continuity with the blastema of the process. This continuity is effectuated by means of a somewhat scarcer blastema than that of the palatoquadrate proper and of the trabecula. The dorsomedial surface of the tip of the palatoquadrate is well separated from the trabecula.

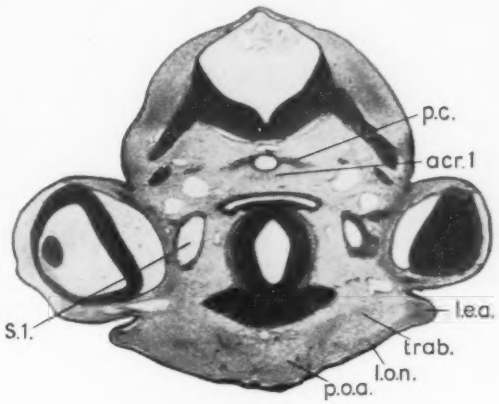

Fig. 48.

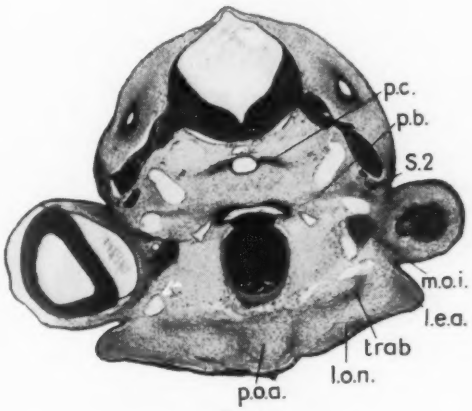

Fig. 49.

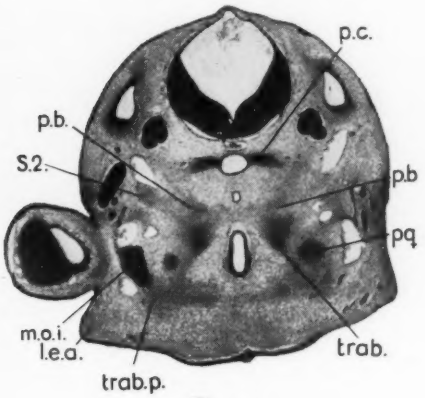

Fig. 50.

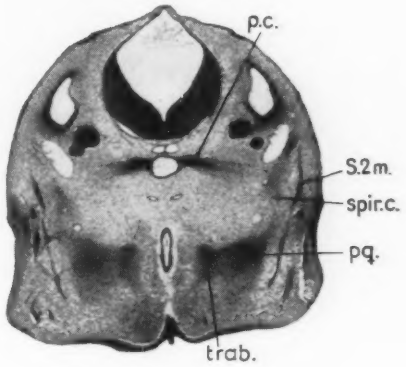

Fig. 51.

Figs. 46—51. *Squalus*. 24.5 mm. Transverse sections of the head region.

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A few sections posterior to the tip of the palatoquadrate, its connection with the trabecula is closer on the medial side and this connection extends along the entire trabecula, but disappears where the trabecula caudally bends dorsad to join the polar cartilage. As the trabecula in early stages develops independent of the palatoquadrate, the very early joining of the two structures may be considered a primary fusion. Already rostral to the point where the palatoquadrate is relatively free from the trabecula, the dorsolateral margin of its blastema extends a broad but thin dorso-lateral lamella (figs. 43, 45, 51, *spir.c.*) which rises towards the ventrolateral part of the auditory capsule to the prespiracular area (fig. 41, *p.sp.a.*). The efferent pseudobranchial artery lies inside this lamella and the musculus constrictor dorsalis (fig. 51, *s.2.m.*) outside. Dorsally it comes outside the jugular vein and the facial nerve. Here it is condensed rather distinctly, forming the rudiment of the "lateral commissure". In the medium part of this big lamella the prespiracular cartilage will later appear. (The lamella is already discernible in the 16.5 mm stage). Thus the palatoquadrate proper of the 24.5 mm stage is provided with an anterior lamellar part fused with the trabecula and a posterior lamella rising towards the auditory capsule.

The hyomandibula of this stage shows a dorso-ventrally short but fronto-caudally rather long upper part, not well delimited from the rest of the hyomandibula. From this upper part the rudiment of a ligament issues, which is inserted on the upper end of the epibranchial of the first branchial arch. The development of the hyomandibula in sharks, however, will be described more fully in *Etmopterus* and *Scyllium*.

The elements of the branchial arches of the 24.5 mm stage are not yet quite separated from each other.

For the auditory capsule see *Etmopterus!*

Squalus acanthias, stages 25.5 and 26—33 mm.

These stages are somewhat less advanced than the 28 mm stage described and figured by VAN WIJHE. As this very prominent author, however, paid but occasional attention to the skeletal blastemas present, it seems necessary to make some additional statements about them. With modifications related to the further development of the lateral sensory system, the mesenchymatic areas are as in the preceding stage and will not be treated further.

The mandibular and hyoid head cavities are (as earlier) no longer present. The lateral part of the appendix (fig. 54, *s.2.*) (the remains of the mandibular somite) of the polar body (*p.b.*) is about to disperse in the general mesenchyma behind the eye and below the jugular vein. The medial part, however, is retained, as a thin lamella extending toward the dorso-lateral border of the palatoquadrate. The efferent pseudobranchial artery runs immediately inside (ventral to) this membrane and enters the brain-cavity dorsal to it.

The premandibular somite is still present showing, however, very interesting and important changes. Its commissure is solid as before, lying below the acrochordal tissue. It is very distinctly separated from this tissue. The premandibular cavity of each side is about to be filled in with cells (fig. 52, *s.1*), apparently chiefly derived from its own wall, but it is also possible, that cells from the surrounding mesenchyma penetrate into the cavity and help fill it with a mesenchymatic network. (Compare, however, *Torpedo* page 208.) The thickening of the wall begins at the commissure and inside the eye muscle rudiments of the anterior part of the somite. In this part only a tubelike lumen is left in the somite. This lumen lies at the lateral side of the triangular somite, the lateral wall of which lies close to the eye-bulb. The dorsal wall is thickened more caudally, whereas the lateral and medial walls are thin. Where the somite touches the eye, the embryonic sclera of the eye is modified owing to cells which outwander from the somite wall (fig. 52, *m.sc.*).

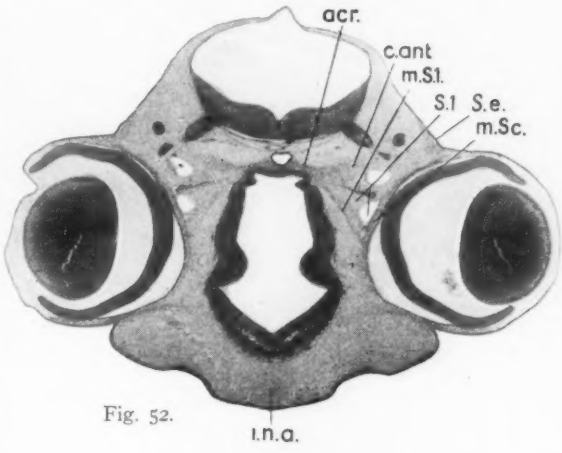

Fig. 52.

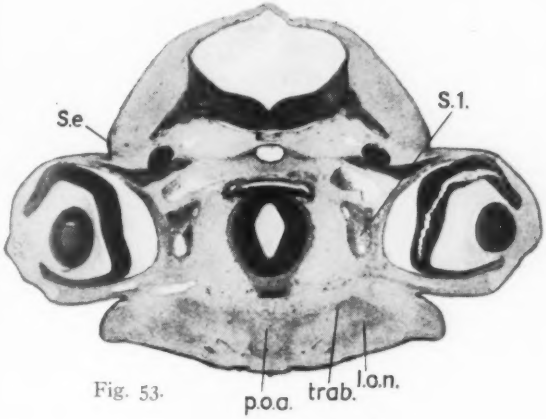

Fig. 53.

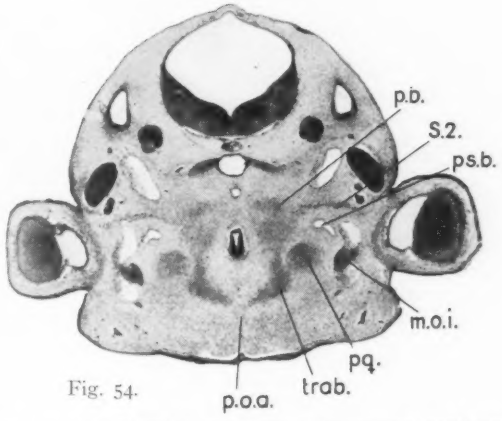

Fig. 54.

Figs. 52—54. *Squalus*. 25.5 mm. Transverse sections of the head region.

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Already in earlier stages the epithel-like wall of the premandibular cavity has produced basally a thin sheet of collagenous fibres enveloping the somite. In the 25.5 to 27 mm stages this sheet is especially well developed on the medial and dorsal sides of the cavity, where, owing to the filling in of the cavity with mesenchymatic cells, these collagenous lamellas have become widely separated from the lumen of the somite (fig. 52, *m.s.1.*) forming relatively independent membranes. The dorsal of these membranes is closely connected with the eye-muscle rudiments, forming an embryonic surface of origin for these muscles. In a 30 mm stage this collagenous membrane is clearly discernible and has thickened considerably. In addition it has become shorter (as the eye has developed mediad). Now it is possible to determine that this membrane will form a tendon of origin to the eyemuscles. Medioventral to this tendon and to the eye muscles, the mesenchyma filling the space, previously occupied by the premandibular cavity, has become condensed to a dense blastema extending between the eye and the acrochordal tissue at the basis of the pila antotica (cartilago antotica) (fig. 52, *acr.*). This blastema of the premandibular somite is the rudiment of the eye stalk (fig. 52, *s.1.*). In the 33 mm stage it is already a short cylindrical dense mass of cells connecting the eye with the basis of the pila antotica. *They eye stalk is thus somitic in origin, developing from the premandibular somite.*

The medial wall of the premandibular somite also makes an important development. Its collagenous membrane (fig. 52, *m.s.1.*), described previously, develops in the 30 and 33 mm stages to a rather thick membrane connecting dorsally with the pila antotica and the orbital cartilage and ventrally with the polar cartilage and the posterior part of the trabecula. Along the pila antotica it seems (in the 33 mm stage) to extend past the trochlear foramen, but it is probable that this frontal extension along the orbital cartilage depends upon a secondary growth of the lamella through the addition of mesenchymatic cells presumably of ectodermal origin. But the formation of this membrane begins with the mesial wall of the premandibular somite, and the membrane described in the preceding closes the brain cavity on its lateral sides, forming the medial orbital wall from the parachordals to the optic nerve. *At least the hind part of the orbital wall thus is formed from the premandibular somite.*

In *Cladodus hassaicus* Stensiö (1937) has found an orbital area devoid of lime-prisms between the opticus and trigeminus exits and developed in relation to the eye-stalk. This area he names the eye-stalk area. A similar area seems to have been present also in *Cladodus wildungensis* (Gross, 1937). It seems possible that this area could answer to the somite part of the orbital wall, developed from the premandibular somite which simultaneously is the origin of the eye-stalk.

The dorsal wall of the optic canal is formed by the medial lamella where it passes ventrally over into the earlier formed collagenous lateral wall of the premandibular cavity.

In the preceding stages no detailed description was given of the medail area. Here some particulars will be given, as the differentiation of this area has gone so far that its future is at least obscurely outlined. Beginning from behind, where the area curves up towards the hypophysial stalk, we find the superficial part of the area very narrow, compressed between the palatine processes of the palatoquadrates and there forming a primitive symphysial tissue. Between the hindmost angles of the trabeculae (fig. 54, *p.o.a.*), this compressed part of the area enters as a thin lamella. Inside the trabeculae the area widens to a connective tissue mass gradually flattening laterally to embrace the brain from behind (below). The cells of this meningeal part of the area are elongated in a transversal direction as are likewise the cells of the hindmost part of the superficial layers of the area and those of the symphysial part. Where the medial area anterior to the symphysis of the palatoquadrates assumes a more horizontal position the superficial parts of the area contain densely crowded mesenchymatic cells lying on the medial line of the head between the parallel infraorbital lines. The deeper parts of the area spread laterad partly to connect with the medial borders of the trabeculae and partly to enter between them, forming part of the connective tissue upon which rest the ventro-posterior parts of the 'tween-brain. Anterior to the trabeculae the area behaves in a like manner with a relatively narrow dense superficial blastema from which the deeper parts extend laterally as a wing on each side (fig. 53, *p.o.a.*) embracing the ventral part of the brain past the future optic nerve. Between the nostrils the superficial part of the internasal area broadens considerably, forming a dense-celled plate between the anterior tips of the infraorbital sensory lines, to attain ultimately the mesenchymatic field (frontal area) inside the glandular field in front. The deeper parts of the medial area always form a bed upon which the brain rests. The superficial part flattens out as it approaches its anterior limit and the deeper parts of the area here merge indefinitely with the deeper layers of the glandular area of which the superficial dense-celled portion merges without demarcation with the superficial parts of the mesenchyma of the medial area. It is already obvious from the stage 25.5 mm that the medial area forms a part of the future wall of the cranial cavity and part of the adjoining meninges.

An examination of the stages 25.5—33 mm makes it evident that the early embryonic medial areas, the preoral, the internasal and at least part of the frontal areas, will in the end form an unity of which the preoral part forms a medial ventral keel on the basis cranii, the internasal, the internasal septum, and the posterior part of the frontal, the rostral plate of later stages.

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The system of acrochordal, polar and trabecular cartilages is somewhat more advanced than before. The trabeculae and polar cartilages, however, have fused (fig. 54), but there is still a considerable gap between the polar cartilage and the acrochordal. The cartilago antotica and the orbital cartilage,—the pleurosphenoid cartilage of VAN WIJHE—,form an unity in which the two components can no longer be discerned. The posterior (cart. antotica) (fig. 52, *c. ant.*) part of the system is connected with the acrochordal tissue and the anterior part merges into the rather thick mesenchyma above the anterior part of the eye at approximately the point where the obliquus superior muscle is inserted. The orbital cartilage of the 25.5 mm stage is a compressed rod, posteriorly prochondrial, anteriorly by degrees more blastematic. Along its entire length the rod is connected with the orbital area by a strand of mesenchymatic cells along which the rod broadens to become a more or less perpendicular plate, as seen in the 26—27 mm and later stages of development.

In the 33 mm stage the frontal end of the orbital rudiment is already bent down so far that it reaches the frontal end of the lamina orbitonasalis. This condition is already discernible in the 30 mm stage.

The eyebrow area of mesenchyma widens antero-dorsally to form the rudiment of the epiphysial bridge. Antero-ventrally it is broad and sends out a tongue of mesenchyma anterior to the nasal sac. This tongue bends around the forebrain and ventrally reaches the medial area. The big rostral bend of the supraorbital sensory canal is located outside the broadened part (prenasal area) of the eyebrow area.

The superior eyebrow area, flat in preceding stages, begins in the 25.5 mm stage to bulge out, forming the superior eyebrow of the fish (figs. 52, 53, *s.c.*). This area at the anterior border of the eye contains a dense mesenchyma which in the 30 mm stage forms a rounded prochondrial body lying lateral to the ophthalmicus superficialis nerve. This body is the rudiment of the socalled preorbital process (or cartilage). It is confluent from the 30 mm stage with the mesenchymatic mass on which the obliquus superior muscle is inserted. The mesenchyma of the supraorbital part of the eye-brow area in the 30 mm stage is ready to arrange itself to form the rudiment of the supraorbital crest, a rudiment which, however, is still quite undeveloped, mesenchymatic. The mesenchyma of the preorbital process will later form the foremost part of the supraorbital crest, which develops from front to back.

The lamina orbito-nasalis rudiment narrows considerably between the eye and the nasal sac. In the 30 mm stage the narrowed part extends further frontad and enters as a lower eyebrow area between the nasal aperture and the eye, already forming a rudiment of part of the anterior wall of the orbita, meeting in the 33 mm stage the orbital cartilage rudiment anterior to the posterior aperture of the orbitonasal canal.

The development of the auditory capsule in *Squalus* was not followed in detail. As it does not differ, however, from that of *Etmopterus*, of which a detailed description is given later, I refer to this description.

Only a few remarks concerning the development of the visceral skeleton in these stages will be given, the reader being here also referred to the description of *Etmopterus*.

In the 25.5 mm stage the connection between the trabecula and the palatoquadrate is loosening but there is still present a connecting mesenchyma between the two elements. The complex of the prespiracular cartilages is as in the 24.5 mm stage.

In the 30 mm stage, where the trabecula as well as the palatoquadrate are chondrified, the connecting blastema is still present, but as the palatoquadrate has somewhat retired from the trabecula, this blastema has been drawn out to a thick lamella, which in the 33 mm stage has become thinner.[1] The upper end of the prespiracular cartilage complex is now inserted on the auditory capsule dorsal to the jugular vein and the hyomandibular nerve and on the basiotic lamina below this vein and nerve, forming the lateral commissure. The prespiracular cartilage itself is present as a big undifferentiated mesenchymatic mass.

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Squalus acanthias, stages 38 and 39 mm.

In the occipital and otical regions the paracordals begin to unite below the notochord (fig. 71). They are (since the 25.5 mm stage) fused laterally with the preotic part of the basiotic lamina. Polar cartilages (figs. 55, 56, 61—63, *p.b.*) and trabeculae are continuous with each other, but not as stated by HARRISON, with the lateral borders of the parachordals. On the contrary they unite only with the acrochordal tissue (figs. 55, 63, *acr.*) not yet chondrified. The orbital cartilages (figs. 55—63, *orb.c.*) are also united with the acrochordal tissue (fig. 62, *acr.*) and, at least frontally only by means of this tissue, with the parachordals. The polar fenestra (fig. 56, *p.f.*) resulting from the medial connection of the anterior platelike parts of the trabeculae by means of the medial area, is narrowed to a posterior medial slit from which a posterior foramen carotideum has been separated by the praecarotid commissure of the polar bodies (fig. 63, *prc.*). Dorsal to this foramen both polar cartilages are now connected by another cartilaginous bridge, the commissura postpituitaria (figs. 56, 63, *pit.c.*) (DE BEER, 1931) just below the notochord and separated from it by a mesenchymatic layer belonging to the acrochordal tissue (fig. 63, *acr.*). Ventral (anterior) to the inner carotid artery lies the praecarotid commissure already mentioned (DE BEER, 1931). The postpituitary commissure is the

[1] The relations between the palatoquadrate and the trabecula are discussed in a following part of this work, where also additional descriptive material is recorded.

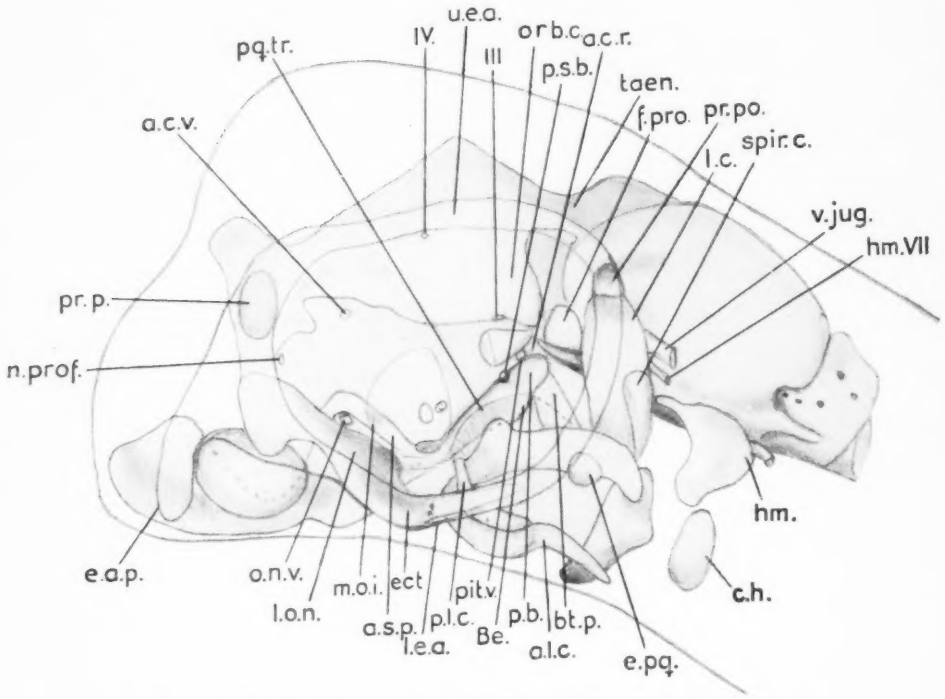

Fig. 55. *Squalus*. 38 mm. Reconstruction of the skull. Lateral aspect.

thicker and develops at first (according to HARRISON in the 35 mm stage). According to VAN WIJHE the praecarotid commissure has a separate rudiment. This is a small rounded cartilage connected by procartilaginous strands with the postpituitary bridge. The unpaired part of the carotid artery, after passing the carotid foramen, divides into two branches in each of which the efferent pseudobranchial artery opens. This artery (fig. 55, 61, *ps.b.*) passes through a notch at the anterior, dorsal border of the polar cartilage. The pituitary vein (figs. 55, 63, *pit.v.*) passes dorsal to the caudal end of the polar cartilage. The trabeculae in a 39 mm specimen as in earlier stages consist of a posterior part, forming almost a right angle with the parachordals, and a more horizontally directed anterior part. (In a 38 mm specimen the trabecula is straighter.) The limit between these two parts, the "Basalecke" of GEGENBAUR, is accentuated by a trabecular process extending caudad (also present in the 38 mm stage) and situated at the level of the polar fenestra.

In the 24.5 mm stage the m. obliquus inferior is inserted upon the lateral process of the trabecula on which rests the anterior tip of the palatoquadrate. In this stage the anterior ends of the trabeculae are continued frontally by a deep broad part of the medial area. In the 25.5 mm stage the insertion of the muscle has shifted to the lateral border of this area which has consequently

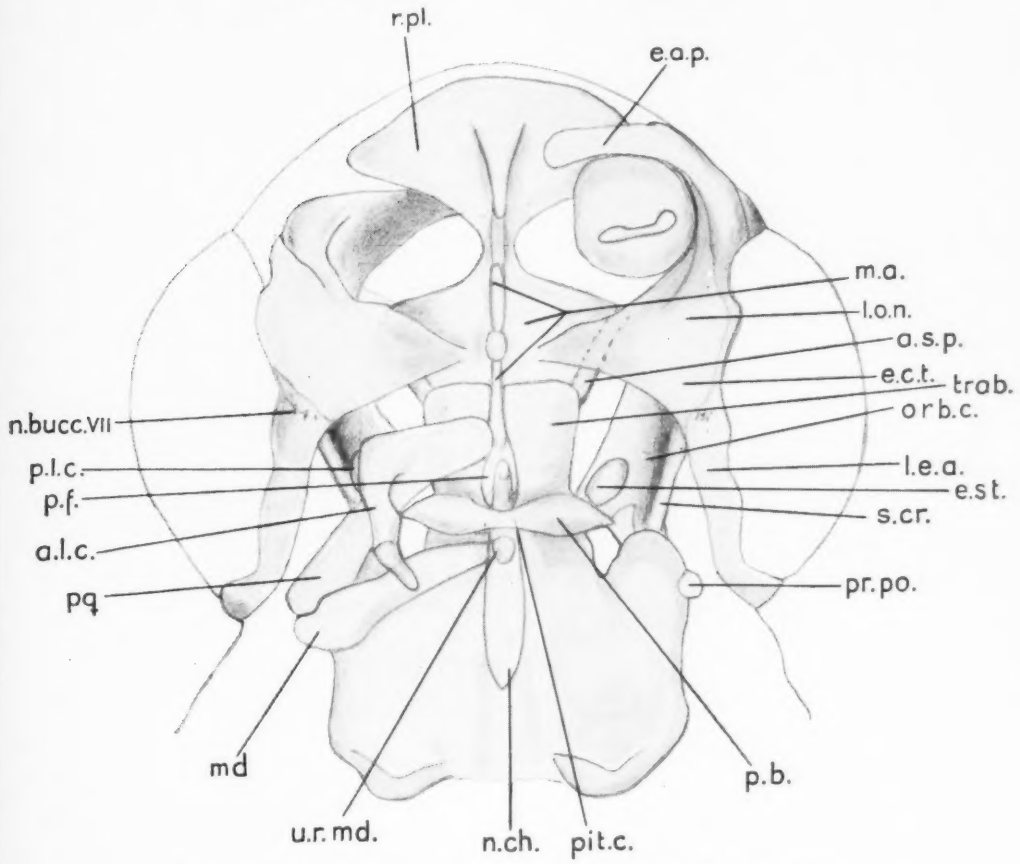

Fig. 56. *Squalus*. 38 mm. Reconstruction of the skull. Ventral aspect.

grown thicker. Then the muscle leaves the trabecula entirely, and the trabecular process disappears (30 mm). In the 38 mm stage this border, with the inserted muscle (figs. 55, 58, *m.o.i.*), is found as a rod caudal to the orbitonasal vein forming "the anterior sideplate" (figs. 55, 56, 58, *a.s.p.*). In front this sideplate joins the frontal broadened part of the orbitonasal lamina.

The medial area posterior to the anterior end of the trabeculae is no longer clearly discernible. The last indistinct remnants of it are seen in the 38 mm stage forming the symphysis of the palatoquadrate and connecting the two trabecular plates in the midline to form the unpaired trabecular plate (figs. 58, 59, *m.a.*). Anterior to the trabeculae the medial area is not only fully formed as in the preceding stages but has grown still more. The deeper layers of the area (fig. 56, *m.a.*) continue the trabecular plate frontally as a medial thick, broad blastema thinning out laterally and supporting the brain. Frontal to the anterior border of the orbitonasal plate this blastematic part narrows

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considerably and becomes rodlike (figs. 55, 57, *m.a.*). On the midline of the said blastematic plate there is found a condensation which soon (39 mm stage) converts into a cartilage of which the posterior parts lie closely to the brain. The rod approches anteriorly the skin between the nasal sacs, lying about midway between the skin and the brain. The superficial parts of the medial area are lacking from behind to the anterior ends of the trabeculae. Frontal to these there is, however, a narrow mesenchymatic lamella joining the deeper parts of the area with the skin, thus forming a medial crista which continues frontad into the frontal part of the medial area. Frontally the medial rod sends out a lamella on each side (fig. 56, *r.pl.*) so that the transverse section of the area becomes a Y-form (fig. 57, *m.a.*). In this part (in the 39 mm stage) the chondrifying internasal rod is no longer discernible, the entire structure being blastematic. The Y-shaped part of the medial area is the rudiment of the "internasal septum" of the adult fish. In the 38 mm stage frontally follows the broad rostral plate, on which rests the forebrain. In front of the forebrain and upon the frontal part of the plate rests a very thick mass of loose connective tissue forming the deep part of the mesenchyma of the glandular epithelial field, which is no longer present. This mass of connective tissue is the rudiment of that gelatinous connective tissue filling in the fossa praecerebralis of the adult shark.

The posterior part of the lamina orbitonasalis is broader than the anterior and forms the rudiment of the ectethmoid process (figs. 55, 56, 58, *ect.*) (Allis, 1923). Anteriorly the lamina becomes narrower and between the eye and the nasal sac it forms a blastematic rod. This rod widens anteriorly and forms a rather big mesenchymatic cell-mass connected dorsally with the orbital cartilage. Between this mass and the broad anterior still remaining superficial part of the lower eyebrow area (fig. 57, *l.e.a.*) runs the ethmoid nerve (fig. 57, *n.et.*). The medial border of the lamina orbitonasalis is not connected posteriorly with the edge of the trabecular plate but with the ventral surface (fig. 58) of the medial area which continues the trabeculae frontad, a little below its somewhat curved up lateral border. The orbitonasal vein (fig. 55, *o.n.v.*) goes medial to the lamina orbitonasalis (figs. 55—58, *l.o.n.*) between it and the "anterior sideplate".

The orbitonasal plate is medially connected by a triangular process (fig. 56) with the medial area somewhat anterior to the tip of the trabecula. The orbitonasal plate, as explained earlier, is developed from the lower eyebrow area, but does not absorb all the mesenchyma of this area, there being left a superficial band of mesenchyma in the lower eyebrow. This band widens frontally considerably above the olfactory sac and sends down a broad process (figs. 55, 56, *e.a.p.*) in front of this sac to join the rostral plate. In the region of the orbitonasal plate the mesenchymatic band of the lower eyebrow area, mentioned above, forms a thickened border of the plate and extends

caudally as a separate structure continuing around the eye. At the point where this caudal extension of the posterior border of the orbitonasal plate begins, it is pierced by small nerve-fibres (figs. 55, 56, *n.bucc.VII.*) belonging to the buccalis VII. nerve.

The dorsal border of the orbital cartilage is bent mediad over the lateral part of the brain. This dorsal part is blastematic. It has a lateral connection only with the connective tissue inside the supraorbital sensory canal. It is about to form a membranous roof above the brain. The rest of the orbital cartilage is more or less vertical (figs. 58—63, *orb.c.*) as is the entire cartilage in the 39.5 mm stage of VAN WIJHE. The limit between the vertical and the dorsally inbent parts of the orbital cartilage forms a ridge along which the mesenchymatic rudiment of the supraorbital crest (figs. 56—63, *s.cr.*) is seen. This rudiment develops from the dorsal (now medial) border of the eyebrow area. The oculomotor nerve passes through a notch near the base of the orbital cartilage (fig. 55, *III.*), between this cartilage and the membranous part of the orbital wall. Dorsal to the trigeminal and facial nerves the orbital cartilage is prolonged backwards forming the taenia marginalis (fig. 55, *taen.*) which has attained the anterior end of the acustic capsule and as a thin blastema may be followed caudad to the blastematic rudiment of the primary postorbital process (fig. 55, *pr.po.*). The foramen prooticum (fig. 55, *f.pro.*) is thus enclosed. The prootic foramen is not a single big foramen as it is closed by a thin mesenchymatic membrane through the ventral part of which the abducens, trigeminal, and facial nerves pass in separate canals. The anterior end of the orbital plate bends down to the tip of the lamina orbito-nasalis. The frontal part of the supraorbital crest blastema thickens and becomes a separate body, the rudiment of the preorbital process (fig. 55, *pr.p.*), inside of which runs the ophthalmic VII. nerve. The rudiment is formed from the eyebrow area.

The lateral wall of the auditory capsule is chondrified in the 39 mm stage. A roof extends from it dorsal to the auditory organ. The medial wall is very incomplete. The posterior independent auditory capsule cartilage of VAN WIJHE is still delimited from the dorsal surface of the lamina basiotica, but has extended around the posterior semicircular canal. It has fused with the lateral wall of the capsule already present as a sparse mesenchyma in the 16.5 mm stage. Between this independent cartilage (the cartilage of KÄLLBERG), and the lamina basiotica passes the glossopharyngeal nerve in a manner which will later be described in *Etmopterus,* where the conditions are something the same, but where a great number of stages have been investigated with special attention to the auditory capsule. From the dorsal edge of the anterior part of the auditory capsule a blastematic rudiment of a tectum synoticum stretches mediad, dorsal to the brain. A little behind the foramen prooticum a small independent prochondrial element lies beyond the

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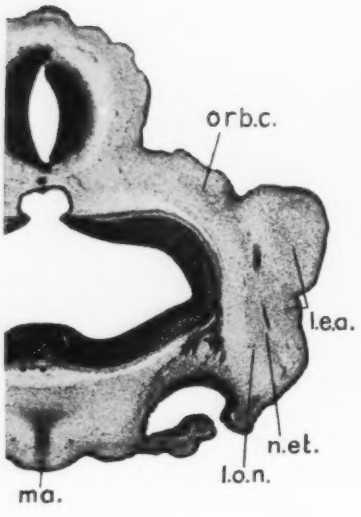

Fig. 57.

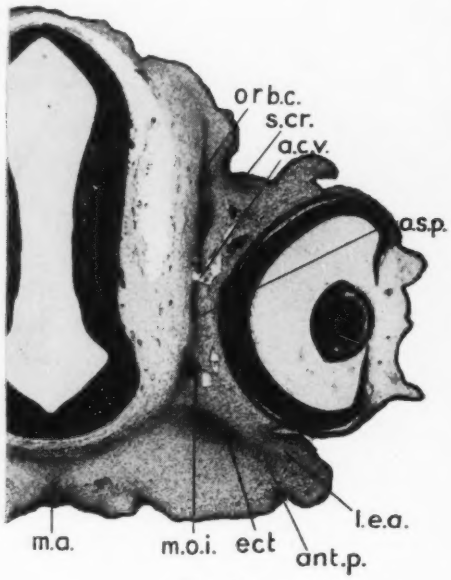

Fig. 58.

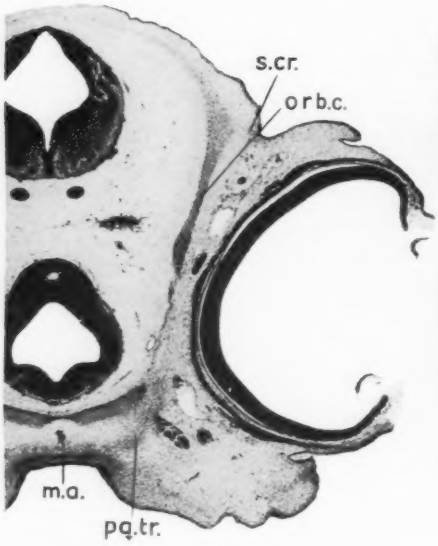

Fig. 59.

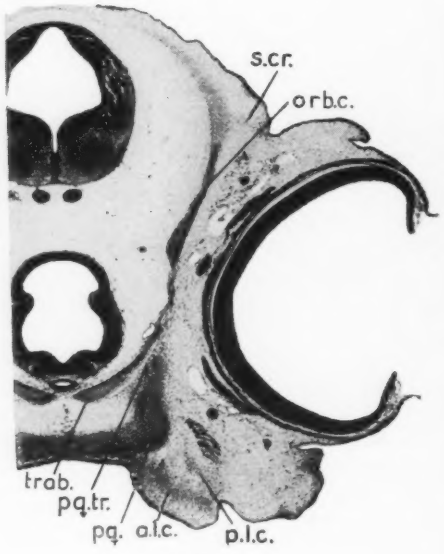

Fig. 60.

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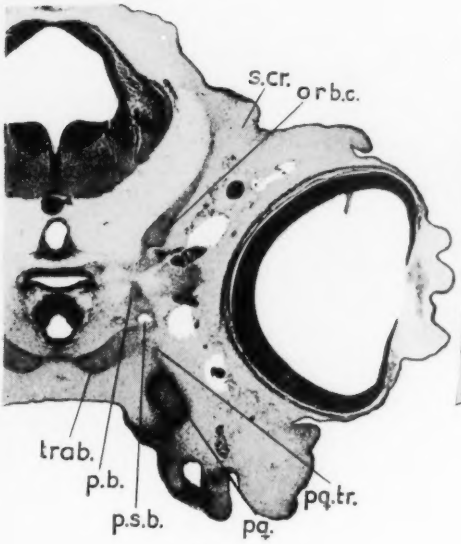

Fig. 61.

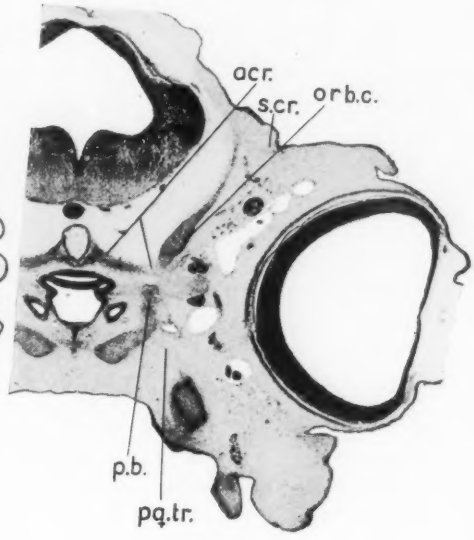

Fig. 62.

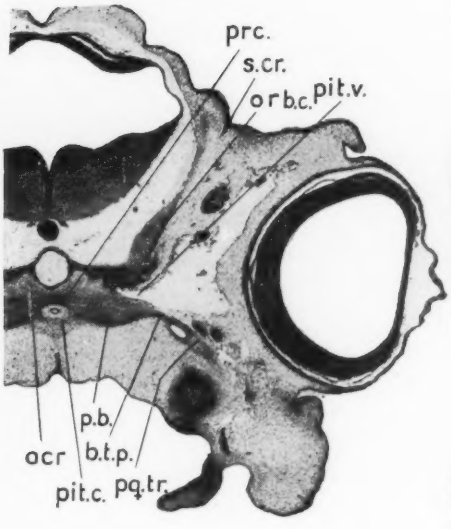

Fig. 63.

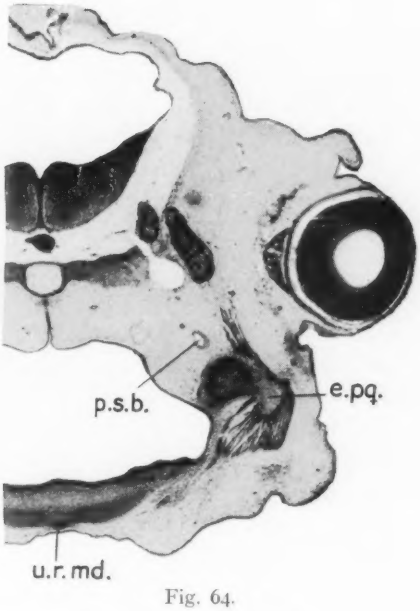

Fig. 64.

Figs. 57—64. *Squalus*. 38 mm. Transverse sections of the head region.

lateral wall. Medial to this rudiment passes a slender nerve branch belonging to the ophthalmicus superficialis *VII*. The rudiment in question is that of the primary processus postorbitalis (fig. 55, *pr.po.*).

Although HARRISON found cartilages of the nasal capsules already present in his 35 mm stage, there are, with the exception of the primary mesenchymatic nasal capsule present in younger stages, no traces of such rudiments in the 39 mm stage here described. The capsule mentioned by HARRISON may be this primary capsule or the rudiment of the lamina orbitonasalis.

The occipital column (pila occipitalis) in the 39 mm stage is not yet fused with the auditory capsule. Anterior to it the vagus nerve issues from the cranial cavity, and posteriorly it is delimited by the first ventral spinal root, which passes through a deep notch in the cartilage of the column. In the specimen examined (39 mm) the occipital column is pierced by four foramina, three for ventral and one for dorsal nerve roots. In the 38 mm specimen there are three ventral and two dorsal roots piercing the column (fig. 55). In VAN WIJHE's 39.5 mm stage only two foramina were present. The first, immediately behind the vagus foramen, in the 39 mm stage passes through a corner of the parachordal plate in front of the column. This nerve corresponds to the occipital nerve X of FÜRBRINGER not existing in VAN WIJHE's 39.5 mm stage. In *Heptanchus* and *Hexanchus* this nerve is present according to FÜRBRINGER (1897). The two other ventral foramina enclose the occipital nerves Y and Z. The fourth nerve, lying dorsal and somewhat behind the foramen of the Z-nerve, is enclosed in the 39 mm specimen by very young cartilage at the upper border of the occipital column. This dorsal nerve has a small ganglion and is apparently the dorsal root of the occipital nerve Z, although no relation between them could be stated. In *Notidanids* and *Heterodontus* this dorsal root is developed in the adult skull. In the former, according to FÜRBRINGER, it passes through an intercalare detached from the vertebral column. It has been embryologically observed in a number of sharks and rays, although its passage through the occipital column as yet has not been demonstrated. The first ventral spinal root of the 39 mm specimen passes dorsal to the first free intercalar. The posterior part of the occipital column shows a close agreement with an intercalar and a basi-dorsal.

The mandibular arch has absented itself from the trabecula and is nowhere in contact with it. By this process, however, the connecting tissue of earlier stages is retained as a ligamentous membrane (figs. 55, 59—63, *pq.tr.*) between the trabecula and the palatoquadrate and in this membrane the big orbital ligament (fig. 60, *pq.tr.*) is differentiating at the upper end of the earlier anterior end of the palatoquadrate which now forms the "orbital process". The membrane extends along the trabecula to the antero-ventral border of the polar cartilage. Its posterior limit on the trabecula is marked by the efferent pseudobranchial artery there curving up to pass dorsal to the

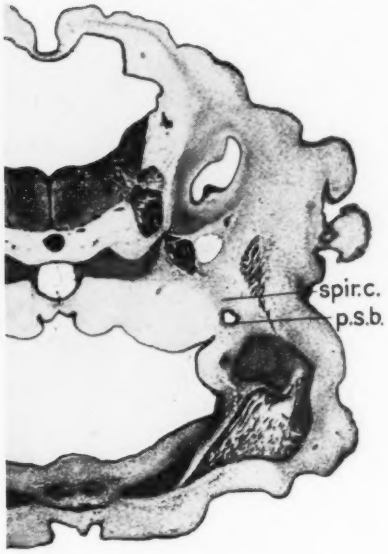

Fig. 65.

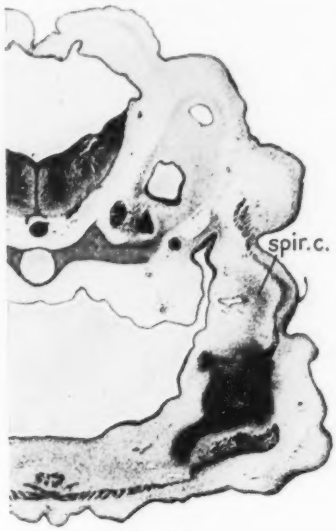

Fig. 66.

Figs. 65—66. *Squalus*. 38 mm. Transverse sections of the head region

boundary between the trabecula and the polar cartilage. The posterior extension of the membrane on the palatoquadrate is longer than on the basis cranii. On the palatoquadrate it may be followed to the prespiracular complex. The posterior part of the anterior lamina thus lies inside the basitrabecular process (see below!), the membrane of which is connected with the posterior part of the anterior membrane. Behind the pseudobranchial artery from the outjutting lateral surface of the polar body issues a membrane (figs. 55, 63, *bt.p.)* which bends down to join the posterior part of the anterior membrane. This membrane from the polar cartilage is the remnant of that mesenchymatic process joining in earlier stages the rudiment of the polar body with the basal part (present as a diffuse mesenchyma) of the muscular process of the mandibular somite. Thus it is somitic in origin. In the 38 mm *Squalus* the polar body membrane lies between the efferent pseudo-branchial artery and the jugular vein. It is limited posteriorly by the facialis and palatinus nerves, the latter bending forwards from behind below the membrane. The orbital artery also passes behind the membrane. These relations seem to indicate that the membrane represents a *basitrabecular (basipolar) process.*

From the posterior part of the palatoquadrate, immediately in front of the articulation part, rises the broad lamella of the prespiracular complex (figs. 55, 65, 66, *spir.c.*). This lamella reaches dorsally the primary postorbital process forming the lateral wall of the jugulo-hyomandibular canal. The ventral wall of this canal is formed by a broad medial process of the complex

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joining the basiotic lamina. The rudiment of the prespiracular cartilage is outlined in the posterior lower part of the complex. The entire complex is still mesenchymatic.

Further structures related to the palatoquadrate are the rudiments of the labial cartilages. Two dorsal and a ventral labial cartilages are present in the adult. They, in the 38 mm stage, are represented by two bent condensations of the mesenchyma of which the anterior (figs. 56, 60, *a.l.c.*) without any boundary issues from the palatin process blastema. The anterior dorsal and the ventral, not yet entirely separated, form a single bent rod in the lips. The posterior dorsal (figs. 55, 56, 60, *p.l.c.*) issues dorsofrontally from the membrane connecting the palatoquadrate with the trabecula.

Finally on the outside of the posterior part of the palatoquadrate, lies a blastematic mass: the rudiment of the insertion tubercle (figs. 55, 64, *e.pq.*) of mandibular muscles. This rudiment (the extrapalatoquadrate rudiments) is already fused to the palatoquadrate, but in earlier stages it is quite separate.

The mandibula has a small unpaired cartilage rudiment (figs. 56, 64, *u.r.md.*) lying in the symphysis.

The hyoid arch contains three pieces: hyomandibula, ceratohyal and "basihyal" extending towards a process of the lower part of the first branchial arch. In the 38 mm stage no branchial rays are developed. The branchial arches consist of S-shaped continuous prochondrial rods. Their upper parts are pierced by vagus branches for the adductor branchialis muscles. The two anterior, in addition, have ventral foramina. The fifth arch is connected by its epibranchial part with the pharyngo-branchial part of the fourth arch, and the hypal elements of the arches are established. Prochondrial processes bending inward and backward and with blastematic ends issue anteriorly from the lower parts of the arches. The ends of the processes of the first branchial arches meet in the medial line, those of the second do not meet, and those of the third and fourth reach an irregular medial blastema, the rudiment of the copular plate (cardiobranchial). The first branchial arch, as said before, is directed forwards and reaches the ""basihyal".

Squalus acanthias, stages 44 mm (MORI) and 45—50 mm (SEWERTZOFF).

The stage 45—50 mm of SEWERTZOFF is somewhat less developed than the 44 mm stage of MORI. The orbital cartilage is connected caudally with the auditory capsule by a taenia marginalis, dorsally closing the fissura prootica to form the foramen prooticum. This foramen is divided into an anterior part for the trigeminal and a posterior for the facial nerves. MORI stated that in the 44 mm stage the bridge separating the two nerves is incomplete. In this stage also the abducens nerve is separated from the foramen prooticum and leaves the brain cavity by way of a small foramen ventral to the trigeminal. In SEWERTZOFF's stage the supraorbital crest is well pro-

nounced. It goes from the auditory capsule frontad and bends down in front of the eye, forming the preorbital crest and it is said by HARRISON to be, in earlier stages, separated from the brain case. Between this crest and the cranial wall passes the ramus ophtalmicus superficialis VII. The slit between the crest and the cranial wall thus corresponds to the praeorbital canal of GEGENBAUER. Through processes from the lamina orbitonasalis ventrally and the orbital cartilage dorsally the anterior part of the orbital wall is said to have formed in front of the optic fenestra. In MORI's figures the arteria pseudobranchialis and the vena pituitaris are enlosed in separate foramina. The latter passes through the "Hirnbodenbucht" of MORI, a canalis transversus not yet being formed. Immediately below the foramen of the oculomotor nerve the eyestalk rudiment is set against the cranial wall. Of the wide polar fenestra there remain only an anterior foramen for the hypophysial stalk and a posterior for the unpaired inner carotid artery. The anterior part of the trabecular plate is bent almost horizontally and the basal corner ("Basalecke", GEGENBAUR) is said to have formed at the bend. The rostral plate is said to be laterally connected with the lamina orbitonasalis, delimiting frontally the fenestra nasalis. In MORI's stage a prochondrial rudiment of a spiracular cartilage and of two superior and an inferior labial cartilage are present. A comparison between these stages of MORI and SEWERTZOFF and the 38 mm stage show that in the latter all structures which characterise the former are present, but that, chondrification has taken place in the former in nearly all places, whereas the skull of the latter is prochondrial (or mesenchymatic).

Squalus acanthias, stages 47 and 48 mm (KÄLLBERG).

The 48 mm stage of KÄLLBERG corresponds rather closely to the 45—50 mm stage of SEWERTZOFF (his fig. 22) but is somewhat less developed than this stage and the 44 mm stage of MORI.

On the ventral side of the notochord the parachordals are connected with each other by a very thin cartilage layer (one cell-layer thick) from the caudal end of the skull to the root of the glossopharyngeal nerve in front. The hook of the notochord is very insignificant. The external notochordal sheath has chondrified from the glossopharyngeal foramen forwards to the region of the polar cartilages. The commissura postpituitaria (fig. 75, *pit.c.*) has fused posteriorly with the parachordals, but it is separated frontally from the notochord by the unchondrified acrochordal tissue (fig. 75, *acr.*) to which are connected the pila antotica (fig. 75, *orb.c.*) and the polar cartilages (*p.b.*). The pila antotica, in addition, is caudally connected with the preotical part of the basiotic lamina and the parachordal plate. The notochord behind the acrochordal tissue thus rests upon a thick cartilage lamella.

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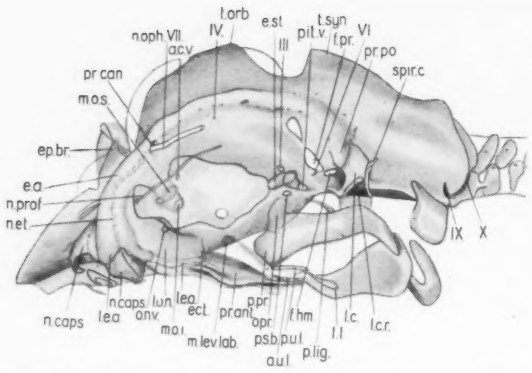

Fig. 67. *Squalus*. 48 mm. Reconstruction of the skull. Lateral aspect.

The trabecular angle against the parachordals (fig. 67) is now about to straighten out, and also the trabecular bend present in earlier stages has straigthened. Its former situation on the trabecula is no longer indicated, but ought to correspond nearly to the point where the m. levator labii superioris is inserted on the trabecula (fig. 67, *m.lev.lab.*). It is evident that the posterior parts of the trabeculae and the polar cartilages have undergone considerable growth in length. The polar cartilages especially have increased and also differentiated in an anterior compressed (fig. 74, *p.b.*) and a posterior broader part (fig. 75, *p.b.*). The latter has a broad triangular process (fig. 68, *p.b.*). A narrow ligament is fastened (fig. 67) at the lateral angle of this process. This ligament (fig. 67, *p.lig.*) extends caudo-laterally to the palatoquadrate where it is inserted at the frontal border of the m. levator maxillae superioris. It is the rest of the lateral appendix of the polar cartilage described in earlier stages. The condition in the 39 and 48 mm stages supports the view that the "appendix" represents a basitrabecular process of the polar cartilage. The trabeculae in the midline are connected with each other by means of the deep part of the medial area, which has chondrified between the two trabeculae. In the 48 mm stage this medial part is well discernable since its cartilage is a little less advanced

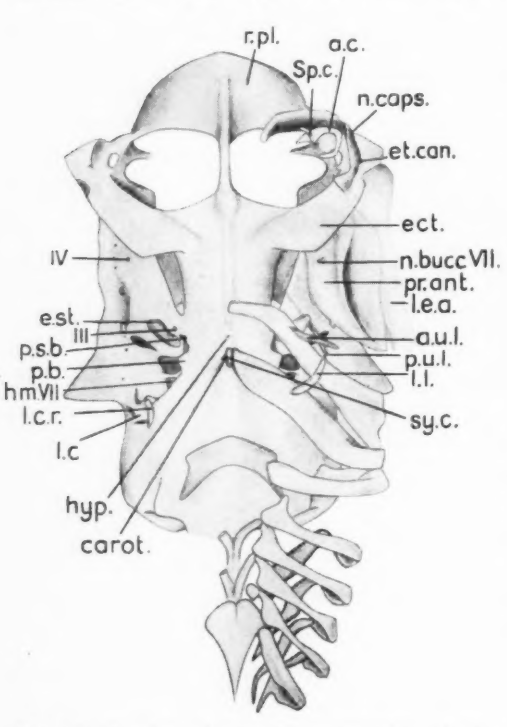

Fig. 68. *Squalus*. 48 mm. Reconstruction of the skull. Ventral aspect.

than that of the trabeculae. In addition it forms a slight ridge in the midline of the trabecular plate (figs. 73, 74, *m. a.*). The incisura of the arteria pseudobranchialis efferens is closed in to a foramen (figs. 67, 68, *psb.*) by a broad cartilaginous plate formed in the membranous cranial wall, probably originating from the premandibular somite as described before. This plate, anterior to the oculomotor foramen (figs. 67, 68, *III.*) and the efferent pseudobranchial artery, is the posterior sideplate of the trabeculae (MORI). A thin cartilaginous lamella thus separates the foramen of the pituitary vein (fig. 67, *pit.v.*), viz., the opening of the future interorbital canal (canalis transversus), from the oculomotor nerve foramen. Beyond the anterior part of the wide pituitary foramen lies the independently chondrifying columnar eyestalk (figs. 67, 68, 74, *e.st.*). It is connected with the acrochordal tissue in front of the pila antotica and the pituitary foramen. The pila antotica is anteromedially connected with the acrochordal tissue, not yet chondrified. Posteromedially it is fused with the parachordals and the preotical part of the lamina basiotica. The polar cartilages are also connected with the acrochordal tissue.

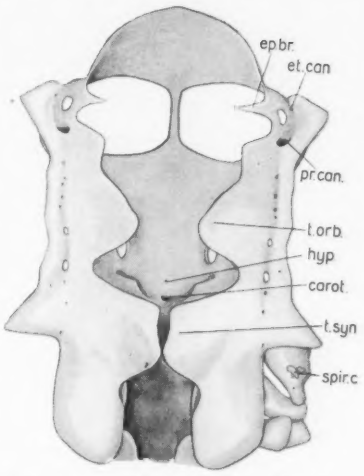

Fig. 69. *Squalus*. 48 mm. Reconstruction of the skull. Dorsal aspect.

In the anterior part of the skull great changes have taken place. The lamina orbito-nasalis, the orbital and praeorbital cartilages have fused with each other and also with the anterior part of the rest of the eyebrow area (fig. 67, *l.e.a.*). The lateral corner of the rostral plate (figs. 68, 69, *r.pl.*) has fused with the anterior border of the orbital cartilage in front of the anterior opening of the preorbital canal (*pr.can.*). By this process the anterior limitation of the nasal fenestra has originated. The prochondrial praeorbital element, of which the upper part continues in the supraorbital crest, lies lateral to the orbital and orbitonasal cartilages, connecting them with each other. The ramus ophthalmicus superficialis VII. (fig. 71, *n.oph.VII.*) passes between the orbital and preorbital cartilages, immediately medial to the latter, and then divides into a frontally and a caudally running branch (fig. 67) (the n. ethmoidalis (*n.et.*)). The latter at first runs between the praeorbital cartilage and the lamina orbito-nasalis and then lateral to the latter. The broad anterior

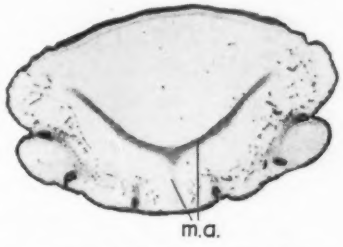

Fig. 70. *Squalus*. 48 mm. Transverse section of the head region.

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part of the lower eyebrow area (fig. 67, *l.c.a.*) is chondrifying. It is fused to the outside of the frontal part of the lamina orbitonasalis. By this fusion the ethmoid nerve (fig. 67, *n. et.*) becomes enclosed in a canal (figs. 68, 69, *et.can.*) (ethmoid canal (GEGENBAUR)). The ramus profundus enters the cranial cavity medial to the praeorbital cartilage (fig. 67, *n.prof.*) and leaves it frontally through a foramen between the rostral plate and the orbital cartilage then following the ophthalmicus superficialis in the anterior part of its grove. The orbitonasal vein (figs. 67, 72, *o.n.v.*) passes through a foramen at the dorsal border of the orbitonasal plate between it and the "anterior sideplate", which is not yet chondrified. The insertion of the obliquus inferior muscle of the eye has shifted to the membranous part of the orbital wall, where it is found together with the obliquus superior on a somewhat condensed portion connected with the orbital cartilage. This portion lies in front of the foramen of the anterior cerebral vein (fig. 67, *m.o.s., m.o.i., a.c.v.*, fig. 72, *m.o.s.*). Of the polar fenestra there remain only (figs. 68, 69) the foramen for the hypophysial stalk (*hyp.*) and that for the carotid artery (*carot.*).

The formation of the foramen prooticum (fig. 67, *f.pr.*) is completed. The supraorbital crest, by way of the taenia marginalis, passes over to the auditory capsule, where it has fused with the small independent cartilage (the rudiment of the primary processus postorbitalis) described in the preceeding stage. Thick connective tissues, continuing caudally the supraorbital crest rudiment of the 38 and 39 mm stages, are about to chondrify in the 48 mm stage, together with the primary postorbital process, now forming the secondary processus postorbitalis (fig. 67, *pr. po.*). Between this process and the auditory capsule pass nerve fibres from the VII. nerve. The supraorbital crest column thus caudally (behind the eye) widens to the big postorbital process fusing to the lateral wall of the anterior part of the otic capsule. But from here the crest column bends round the posterior part of the eye and turns frontad below the eye in the ventral eyebrow area. This part, however, does not chondrify. The column continues uninterrupted to the antero-ventral part of the eye and is here fused to the preorbital cartilage that forms the frontal end of the supraorbital crest. Phylogenetically it seems to be possible, that the eye was once surrounded by a complete exo- or endocranial skeletal ring. In *Macropetalichthys* the orbita is almost completely surrounded by endoskeletal substance and in other Elasmobranch fishes, such as Antiarchi, the exocranial orbital ring was probably complete. I believe therefor that the orbital ring in *Squalus* may represent the remainder of such a complete circumorbital cartilage or bone ring or circumorbital crest. From the pila antotica, somewhat below the taenia marginalis, a new cartilaginous connection or bridge has arisen in the connective tissue membrane between the orbital cartilage and the auditory capsule. This cartilage bridge divides the foramen prooticum in an upper and a lower part. The former becomes

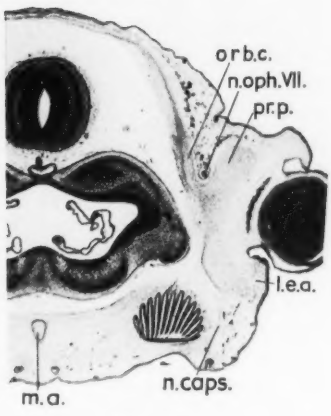

Fig. 71.

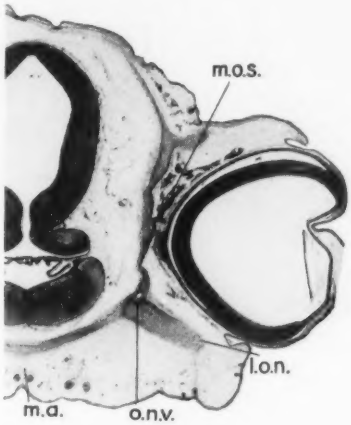

Fig. 72.

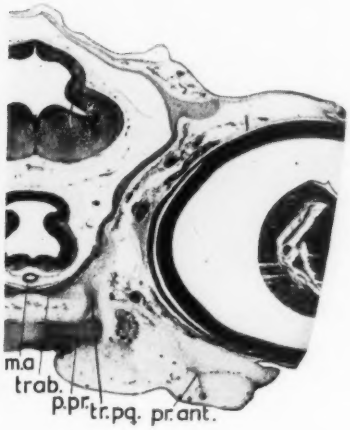

Fig. 73.

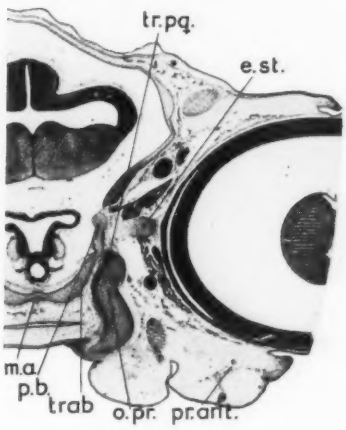

Fig. 74.

Figs. 71—74. *Squalus*. 48 mm. Transverse sections of the head region.

closed, whereas the latter is divided by the commissura praefacialis, already earlier present as membrane, in the anterior trigemino-facialis and the posterior hyomandibularis foramen (figs. 67, 68, *f.hm. hm.VII.*). From the former a special foramen for the abducens nerve is on the point of being (separated and) enclosed by cartilage. (Earlier it was surrounded by membrane.) From the ventral part of the auditory capsule a shelf is forming ventral to the ramus hyomandibularis VII. which faces back. In front of this shelf the ramus palatinus VII. branches off from the ramus hyomandibularis and immediately in front of the shelf the external carotid (CORRINGTON, 1930), or orbital artery passes down to unite with the paired dorsal aorta. Between this shelf and the primary postorbital process the lateral commissure (figs.

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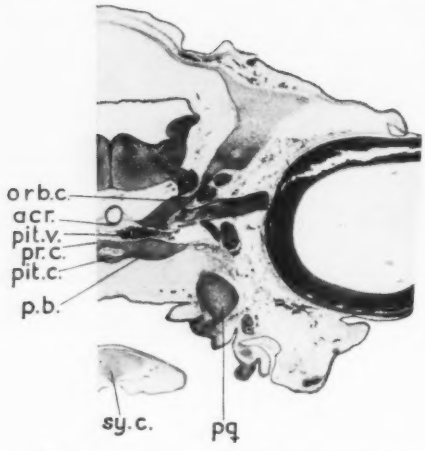

Fig. 75. *Squalus*. 48 mm. Transverse section of the head region.

67, 68, *l.c.*) is present as a connective tissue lamella formed by the upper end of the prespiracular complex earlier covering the truncus hyomandibularis and the jugular vein laterally. In the ventral part of the lateral commissure where it borders the mentioned shelf a rodlike chondrifying part (figs. 67, 68, *l.c.r.*) is found. This rod may probably be considered a mandibular ray belonging (?) to the prespiracular complex. Two real prespiracular cartilages are present (figs. 67, 69, *spir.c.*). The posterior auditory capsule cartilage has fused with the lamina basiotica.

The dorsal part of the occipital column has fused with the auditory capsule, thus forming the vagus foramen (fig. 67). The vena cerebralis posterior passes through this foramen on its way to the vena capitis lateralis (jugular vein.) The occipital column is pierced by three ventral occipital nerves, all entering the vagus canal. The dorsal roots of Y and Z and their foramina have disappeared. From the posterior ventral part of the occipital column issues a caudally directed process which extends to the lateral side of the first free basidorsal piece. The dorsal spinal roots are enclosed in their intercalars and the ventrals begin to pierce their basidorsals (fig. 67) (KÄLLBERG).

The cartilaginous roof of the cranial cavity is about to be established. A tectum synoticum (figs. 67, 69, *t.syn.*) nearly connects the auditory capsules anterior to the ductus endolymphaticus. Anterior to this tectum two other plates strive to meet dorsal to the brain in order to form a tectum orbitale (figs. 67, 69, *t.orb.*), and in the region of the epiphysis two slender cartilage processes have formed in the connective tissue bridge earlier present in this region of the skull. These processes will later form the cartilaginous epiphysial bridge (figs. 67, 69, *ep.br.*).

That part of the orbitonasal lamina which is not involved in the formation of the nasal capsule and the preorbital frame forms a shelf below the anterior part of the orbita. It is usually called the antorbital or ectethmoid process (figs. 67, 68, *ect.*, 72, *l.o.n.*). This shelf is laterally continuous with the lower eyebrow area, which, behind its posterior part, is continued in the eyebrow. The shelf in the 48 mm stage is prochondrial whereas the eyebrow area merely contains mesenchyma. The posterior border of the antorbital process is continuous caudally with a long triangular process of pure mesenchyma (figs. 67, 68, 73, 74, 77, *pr.ant.*) which is in continuity with the eyebrow area.

Immediately behind the ectethmoid process this process is pierced by fibres of the sensory buccalis VII. nerve (fig. 68, *n.bucc.VII.*). The triangular process has two high longitudinal ridges, the ventral connecting it with the infraorbital sensory line, the lateral, with the eyebrow area. A third short anterior dorsal ridge connects with the sclera of the eye. In the future development the process becomes ligamentous and thus disappears as a skeletal element in *Squalus*. In the rays as will be shown later, it becomes the so-called antorbital cartilage or fin-supporting cartilage, which is thus not a part of the ectethmoid process in *Squalus*.

The nasal capsule of the 48 mm stage is about to form, its rudiment being quite blastematic. It originates in relation to the orbitonasal lamina which forms its dorso-lateral wall (figs. 67, 68, 71, *n.caps.*). No medial wall is yet present. Its anterior and lateral walls form an unity. The anterior part is a very thin membrane, which is connected with (but not yet quite fused to) the horizontal part of the medial plate (fig. 67). Behind this thin part the lamella thickens and forms the main part of the lateral wall as a broad ventral process from the orbitonasal lamina. To the outside of this part the very thick and broad anterior part of the eyebrow area is fused. Thus the medium part of the lateral wall of the nasal capsule appears very thick. Behind this part the lateral wall is again thinner and fastened (fig. 68, *n.caps.*) to the lower side of the anterior part of the lateral process of the lamina orbitonasalis. Thus the secondary nasal capsule is primarily related to the orbitonasal lamina, but forms *in situ*.

The palatoquadrates are chondrified allthrough. Their palatine processes (figs. 67, 73, *p.pr.*, 68) are frontally connected with each other by a thin lamella of symphysial tissue derived from the medial area. The orbital process (figs. 67, 74, *o.pr.*) is well developed. The connection of the palatoquadrate with the trabecula is not greatly altered from that of the 38 mm stage, but is about to be transformed into a fascia (fig. 73, *tr.pq.*). In the region of the orbital process this fascia (fig. 74, *tr.pq.*) is transformed to a ligament which is longer than the breadth of the fascia and is therefore bent double. The "basitrabecular process" forms a ligament connecting the polar cartilage with the palatoquadrate in front of the prespiracular complex (fig. 67, *p.lig.*). Two upper and one lower lip cartilage are present. The anterior upper (figs. 67, 68, *a.u.l.*) is connected with the palatoquadrate, the posterior upper with the trabecula in front of the palatoquadrate (figs. 67, 68, *p.u.l.*). These connections are in accordance with their origin, as it was described in the 38 mm stage. The lower lip-cartilage (figs. 67, 68, *ll.*) is segmented off from the anterior upper cartilage.

In the lower yaw an unpaired medial cartilage (figs. 68, 75, *sy.c.*) forms the symphysis.

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The hyoid arch is much as in the preceding stage. Hyoid rays, however, are present.

The branchial arches (fig. 68) are well chondrified, with differentiated pharyngo-, epi-, cerato- and hypobranchial elements. The hypobranchials of the second and third arches meet in the medial line.

Squalus acanthias, stage 59 mm (KÄLLBERG).

This stage corresponds almost entirely with the 60 mm stage of HARRISON. The parachordals are now in their entire length fused below the notochord.

The different nerve- and bloodvessel- foramina begin to receive their definite dimensions. The optic fenestra, however, is wide, but has diminished considerably because of the development of the anterior sideplate of the trabeculae (MORI). These had already begun their development in the preceding stage. Through these sideplates (fig. 76, *a.s.p.*) the membranous orbital wall of the "optic fenestra" becomes divided in an anterior and a posterior part, of which the anterior should be entirely closed according to MORI. The fact is, however, that the ramus profundus V. (fig. 76, *n.prof.*) makes its way through this part of the wall. Thus there remains the profundus foramen. Immediately behind the anterior sideplates of the trabeculae there is present in the chondrified part of the orbital wall (fig. 76, *a.c.v.*) an incisure for the vena cerebralis anterior. This incisure later encloses and becomes a foramen for the anterior cerebral vein. The orbitonasal canal (fig. 76, *o.n.v.*) pierces the cranial wall between the lamina orbito-nasalis and the already chondrified part of the orbital wall (anterior sideplate). Thus the anterior sideplate of the trabeculae lies between the vena cerebralis anterior posteriorly and the vena orbito-nasalis and the nervus profundus anteriorly.

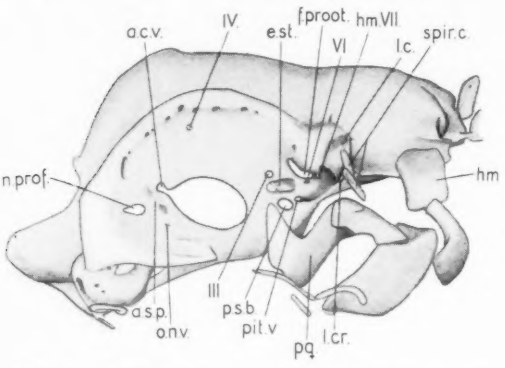

Fig. 76. *Squalus*. 59 mm. Reconstruction of the skull. Lateral aspect.

The pituitary vein is not yet enclosed in a cartilaginous canal (transversal canal, interorbital canal). Cartilage for the enclosing of the vein, however, is about to appear, in connection with the postpituitary commissure. From this commissure a process extends frontad below the vein. This process is laterally connected with the polar cartilage region by prochondrial strands immediately in front of the pituitary vein. From the pila antotica, dorsal to the vein, short mediad directed "processes" have arisen. These are the rudiments

of the dorsum sellae the anterior border of which consist of the acrochordal tissue immediately in front of the pituitary vein. This tissue chondrifies from the processes mentioned above. In an 84 mm stage these processes have met medially to form a "prootic bridge" (commissura prootica, DE BEER) below the notochord.[1] In this stage of development the polar cartilages, the eyestalks and the anterior portions of the basal parts of the pila antotica are fused with each other through chondrification of that part of the acrochordal tissue which in the preceding stage was still unchondrified (fig. 76). The lateral commissure is largely as in the preceding stages (figs. 76, 78, *l.c.*).

Fig. 77. *Squalus*. 48 mm. Transverse section through the region of the antorbital process.

The roof of the brain cavity of this stage does not agree with that of HARRISON'S stage. No pineal foramen is present as the cartilaginous epiphysial bridge is not yet complete. The tectum orbitale has chondrified and is nearly fused with the tectum synoticum. A blastematic part, however, shows the limit between these two components of the roof. In the medial line between the lateral parts of the tectum orbitale a thickened part surrounded by young cartilage gives evidence for the interpretation of this part of the roof, except for the two orbital lamellae, as originating from a medial independent rudiment. The "posterior fontanella" of HARRISON has not yet closed caudally. The two occipital columns strive to meet dorsal to the brain to form a tectum posterius.

The nasal capsule is now completed by a mesenchymatic medial wall (fig. 78, *m.n.caps.*) developed in connection with the rostral plate. The medial wall rudiment is about to divide the primary nasal fenestra into the medial subnasal ("Basalkommunication", GEGENBAUR) and the secondary or the nasal fenestra proper.

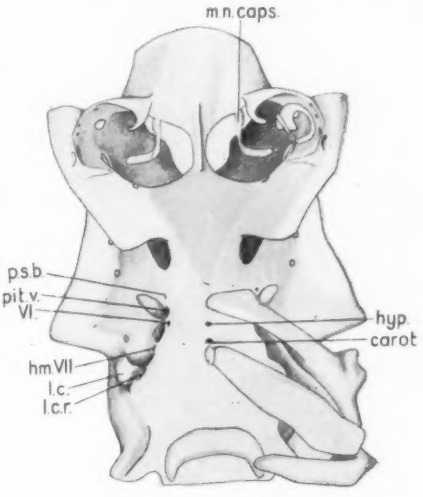

Fig. 78. *Squalus*. 59 mm. Reconstruction of the skull. Ventral aspect.

[1] This bridge and the "processes" forming it are chondrified parts of the acrochordal tissue.

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With this stage all essentials of the adult skulls are established. In the further development the roof of the skull becomes complete, the hypophysial foramen closes in its position near the carotid foramen and other details which will not be mentioned here are elaborated.

ETMOPTERUS SPINAX (Spinax niger).

A continuous description of the cranial development of *Etmopterus* (Spinax) has never been published. BRAUS (1899) and K. FÜRBRINGER (1903) however, have investigated some questions especially concerning the occipital region and the spiracular cartilages. In order to ascertain that the development of the skull of *Squalus acanthias* given in the preceding pages really reflects conditions characteristic at least of squaloid sharks and not eventually is peculiar to this species of shark alone I have undertaken an investigation upon thirteen successive stages of *Etmopterus spinax,* in the biggest of which the development of the skull is principally completed. As the early development is in all essentials similar to that in *Squalus* only a few remarks will be made about the stages 11, 13, 15, 22.5 and 24 mm.

Etmopterus spinax, stages 11—15 mm.

These young stages of development differ so little from those af *Squalus acanthias* that it is not necessary to give any description of them. One difference is, however, that the rudiments of the sensory line placodes of the head are much broader than in *Squalus.* There are also some slight differences in the arrangement of the sensory lines, which, however, will not be mentioned here [compare RUUD (1920)]. The 11 mm stage shows much the same advancement as the 12.5 mm stage of *Squalus.* The trigeminal sensory line placode is, however, lacking. The 15 mm stage is not as far advanced as the 16.5 mm stage of *Squalus.* That saddle-shaped envelope of the ventral brain surface at the big flexure of the brainstem, in *Squalus* developing from the mandibular somite, is not discernible in my sections of *Etmopterus,* but nevertheless may be present.

Etmopterus spinax, stages 22.5 and 24 mm.

These stages seem to correspond to 18 and 22 mm stages of *Squalus* respectively. In the 22.5 mm stage the polar cartilage and the trabeculae are present as mesenchymatic condensations without distinct boundaries. Also the mandibular arch is present as a mesenchymatic rod in the interior of the oral arch. Prochondrial tissue is present in the parachordals. A rather dense mesenchyma surrounds the auditory vesicles. The three head cavities are present: the premandibular somite is a big vesicle of which the commissure

is solid or about to dissolve; the mandibular and the hyoid cavities are tubelike. In connection with the development of the rectus externus muscle the hyoid cavity extends some distance towards the eye. In the 24 mm stage the head somites behave as in the 22.5 mm stage. In other respects this stage agrees very much with the 25 mm stage the essentials of which will be described below.

Etmopterus spinax, stage 25 mm.

The mesenchymatic areas are principally as in *Squalus*. The head cavities have disappeared. The premandibular cavity has been filled in with mesen-

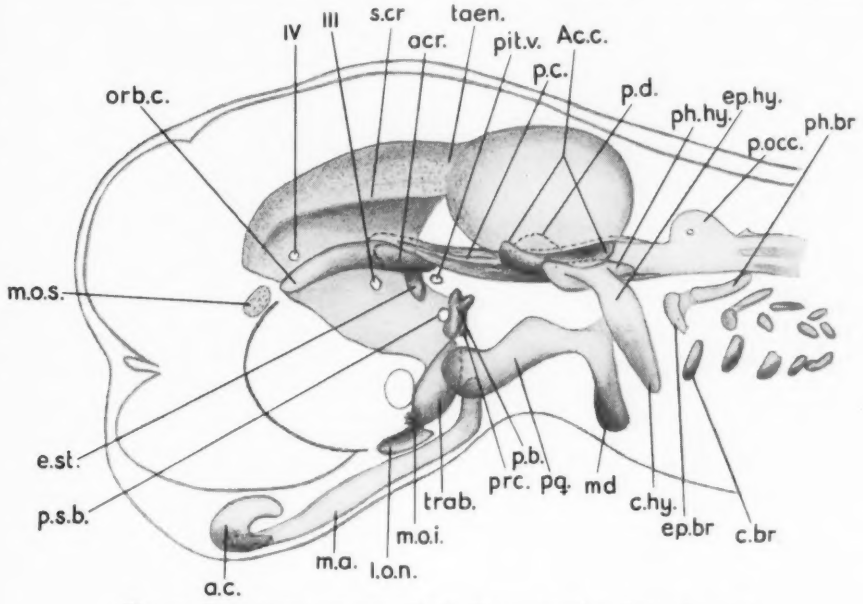

Fig. 79. *Etmopterus*. 25 mm. Skull. Reconstruction. Lateral aspect.

chymatic cells, at least partly derived from the walls of the cavity. The outlines of the somite, however, are well discernible and behave as in *Squalus*, the medial wall forming a membranous orbital wall in this region and the lateral adding mesenchymatic tissue to the sclerotic membrane of the eye. The dorsal wall, together with part of the cells in the interior of the former cavity, are condensed and give rise to the eyestalk (fig. 79, *e.st.*) as in *Squalus*.

The anterior end of the parachordals in the 25 mm stage is pointed (fig. 80, *pc.*), the tip lying close to the notochord. The foremost part of the parachordals is uniformly thin. Caudally, however, they thicken towards the notochord and become triangular in transverse section. In the anterior auditory region the parachordal, already chondrifying, is laterally connected with the prochondrial anterior part of the basicapsular lamina (fig. 80, *l.bas.1.*)

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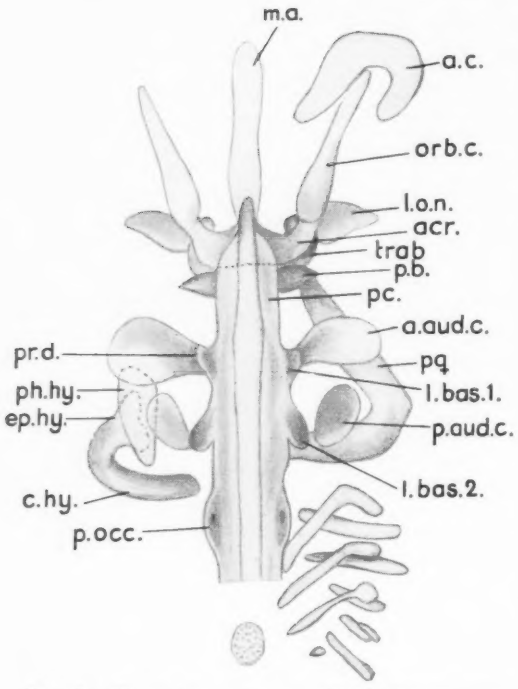

Fig. 80. *Etmopterus*. 25 mm. Skull. Reconstruction. Dorsal aspect.

from the medial border of which a perpendicular lamina rises medial to the auditory vesicle. This lamina (fig. 80, *pr.d.*), the "processus dorsalis" of DE BEER, forms the preglossopharyngeal part of the medial wall of the auditory capsule. The basicapsular lamina laterally is connected with the anterior rudiment of the auditory capsule (*a.aud.c.*). This is, however, only a more advanced part of the already present auditory capsule which is blastematic in its other parts. Behind the glossopharyngeal nerve the posterior part of the basicapsular lamina (fig. 80, *l.bas.2*) and the posterior rudiment of the auditory capsule (*p.aud.c.*) are present. Behind the anterior basicapsular lamina the parachordals become uniformly thick and solid. The glossopharyngeal nerve, leaving the brain cavity behind the dorsal process, passes dorsal to the posterior basicapsular lamina (commissura basicapsularis posterior) and the posterior auditory capsule rudiment. In this stage (as in all the following) the glossopharyngeal nerve undoubtedly runs through the posterior part of the embryonic auditory capsule.

Behind the auditory region of the parachordals, the latter again have triangular transsections. Around the ventral occipital root the blastematic occipital column (figs. 79, 80, *p.occ.*) rises on the parachordals. The nerve thus pierces the column. In the 24 mm stage the occipital column is merely suggested anterior and posterior to the nerve. It thus seems possible that the occipital column in *Etmopterus* consists primarily of two elements only, as GOODRICH has described in *Scyllium*. Behind the occipital column the parachordals continue as a prochondrial lamina on each side of the notochord. The upper border of this lamina is thickened, forming the "obere Basalstreifen" of VAN WIJHE (fig. 79). Already in the 15 mm stage these are suggested and they are there connected with the "unteren Basalstreifen" of VAN WIJHE, which in *Etmopterus* seems to arise together with the "obere Basalstreifen".

The rudiment of the complex polar cartilage + trabecula is located at approx-

imately right angle with the parachordals (fig. 79). The polar cartilage (figs. 79, 80, *p.b.*) is found a good distance ventral to the parachordal and also a good way behind its anterior tip. Frontally (ventrally) the polar cartilage lies in immediate contact with the caudal (upper) end of the trabecula (figs. 79, 80, *trab.*) from which it is, however, well distinguishable as its cells are greater than those of the trabecula. The upper (caudal) part of the polar cartilage is laterally drawn out into a process (fig. 80, *p.b.*) which is continuous with that part of the mandibular somite lying immediately dorsal to the muscular process of this somite, as is the case in *Squalus*. The stages 22.5 and 24 mm show a corresponding connection. The rudiment of the precarotid commissure (fig. 79, *pr.c.*) is connected with the lower cylindrical part of the polar cartilage. The medial part of the commissure seems to have arisen independently, probably as part of the medial mesenchymatic area. The trabecula is somewhat spoonlike. The obliquus inferior muscle (fig. 79,*m.o.i.*) is inserted near its anterior tip. In the 22.5 mm stage this muscle inserts on a low process of the trabecula lying immediately in front of the anterior tip of the palatoquadrate. As the trabecula later grows frontad the insertion also shifts frontad. The anterior ends of the two trabeculae do not reach each other, the deeper parts of the medial (preoral) area entering between them as in *Squalus*. The anterior end of the palatoquadrate rudiment (fig. 79, *pq.*) lies close to the upper half of the trabecula. At the lower (anterior) end of the trabecula an indistinct lamelliform condensation of the mesenchyma announces the existence of the early rudiment of the lamina orbitonasalis (figs. 79, 80, *l.o.n.*). The medial area (fig. 79, *m.a.*) consists, as in *Squalus*, of a superficial rodlike part and a deep part with lateral extensions below the brain, entering posteriorly between the trabeculae, as mentioned above. Particulars about the medial area, however, could not be studied in the younger stages of *Etmopterus*, partly because of the preservation of my material (Zenker's fixation) and partly because of the relative sparseness of cells in these stages of *Etmopterus*.

The pila antotica lies in a straight line with the notochord. They are continuous medially with the acrochordal tissue (figs. 79, 80, *acr.*) underlying the anterior end of the notochord. This tissue thus forms, as in *Squalus*, a commissure of the pila antotica below the notochord. The pila antotica of this stage is prochondrial. As in *Squalus* a broad lamella of mesenchyma joins the pila with the supraorbital area inside the supraorbital sensory line. This lamella and part of the supraorbital mesenchymatic area together form the upper part of the orbital wall, whereas the rest of the area forms the roof of the brain case dorsomedial to the future supraorbital crest (fig. 79, *s.cr*), which in the actual stage is only foreshadowed by the dorsal eyebrow area. The mesenchyma of the supraorbital area continues caudad to the rudiment of the auditory capsule, forming a blastematic taenia marginalis (fig. 79, *taen.*), dorsally closing the foramen prooticum.

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The horseshoeshaped mandibular arch of the 25 mm stage is well outlined, prochondrial, connected with the epithelium of the oral arch by a rather dense and thick blastematic lamella ("teeth mesenchyma"). This blastema is much thicker frontally than it is caudally, and it bends mediad almost to the posterior part of the medial area. This thicker part of the blastema is the young rudiment of the palatin process of the palatoquadrate and the teeth-plates of this process. Ventral to the teethblastema, beginning a little behind the anterior end of the palatoquadrate, another thick superficial blastema is seen. This forms a rod that goes parallel with the mandibular arch round the mouth, to end near towards the middle of the mandibular part of the arch. This blastema is that of the labial cartilages (omitted in the figs. 79 and 80).

As in *Squalus* the blastema of the spiracular cartilages (omitted in the figs. 79 and 80) is connected with the palatoquadrate, and the palatoquadrate, as in *Squalus,* is connected with the trabecula.

The upper part of the hyomandibula in the 22.5 to 25 mm stages is continuous with a broad and elongated blastematic mass (figs 79, 80, *ph.hy.*) lying along the ventrolateral side of the auditory capsule rudiment. This blastema is not distinctly separated from the hyomandibula. Later its medium part takes part in the formation of the upper end of the hyomandibula. Its anterior part seems partly to fuse with the auditory capsule, partly to disappear. Its posterior part transforms to a ligament connecting the upper end of the hyomandibula with the first epibranchial. The said blastema seems to represent a pharyngohyal element, as will be explained later. The lower end of the hyomandibular blastema is denser than the rest of it and continuous with the mandibular arch at the place of the future articulation. The anterior part of the constrictor dorsalis muscle inserts on the lower portion of the hyomandibula.

The ceratohyal and the hyomandibula (fig. 79) are fused in the 22.5 to 25 mm stages.

The two anterior branchial arches are composed of two elements, the two next by three, and the last by two (fig. 79). The pharyngobranchial elements of the two first arches have already fused with the epibranchials, the connection between them, however, being blastematic. The pharyngeal elements of the third and fourth arches are still free. In the fifth arch no pharyngobranchial is present. In the 22.5 mm stage only the three anterior arches are established but they all consist of three separate blastematic elements. In the 25 mm stage an irregular blastematic rudiment of a copular plate is present at the level of the fourth branchial arch.

The visceral arches in *Etmopterus* are thus established as VAN WIJHE has demonstrated in *Squalus* as having separate rudiments of the pharyngo-, epi- and ceratobranchial elements, which however fuse before condrification, forming mesenchymatic units as SEWERTZOFF shows in his fig. 5.

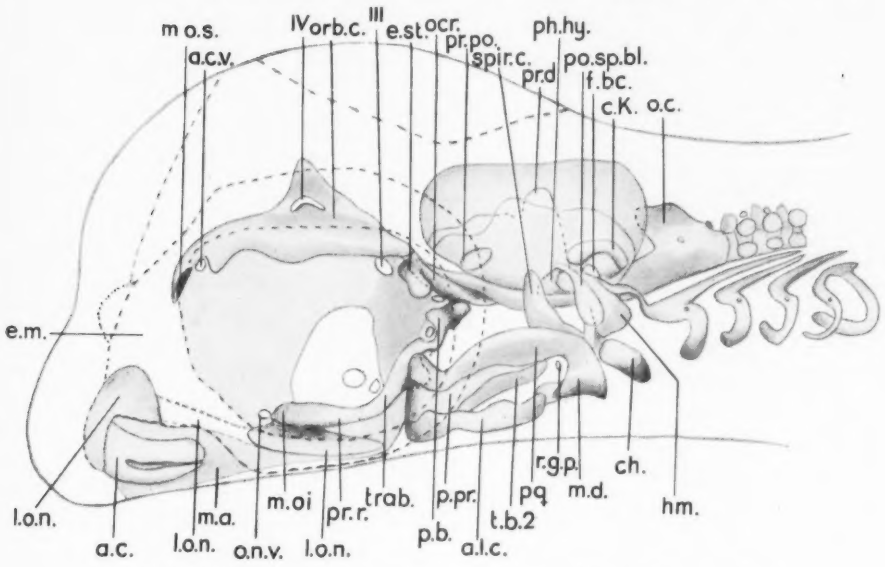

Fig. 81. *Etmopterus.* 30 mm. Skull. Reconstruction. Lateral aspect.

Etmopterus spinax, stage 30 mm.

This stage nearly corresponds to the 35—38 mm stage of *Squalus,* where the rostral plate is forming. It is obvious that in *Etmopterus* the nasal sacs are situated further forward than in *Squalus.* This accounts for the (somewhat) different aspect of the frontal parts of the skull rudiment in *Etmopterus.*

The parachordals are pointed frontally (figs. 82, 83, 84, 85, *pc.*). They extend caudad as cartilaginous bands along the chorda dorsalis. They strive, however, to enclose the chorda especially on its ventral side. The main part of the two rudiments of the auditory capsule are now chondrified or chondrifying. The anterior bends up laterally at the lateral side of the otic vesicle, forming the anterior part of the lateral wall of the future cartilaginous capsule. At the level of the posterior margin of the anterior commissura basicapsularis it reaches the lateral semicircular canal. The lateral wall declines posteriorly and affords a ventrolateral support to the sacculus of the labyrinth organ. From the anterior lateral margin of the auditory capsule cartilage a lamella enters between the anterior semicircular canal and the complex of the facial nerve. This lamella here forms part of the inner wall of the auditory capsule. It extends caudad, dorsal to the acustic nerve to reach an anterior extension of the processus dorsalis (fig. 81, *pr.d.*). The processus dorsalis is now higher than in the preceding stage. The glossopharyngeal nerve runs in an incisure of its posterior margin. The posterior cartilage of the auditory capsule also bends around the labyrinth organ and it has already fused with the posterior basicapsular commissure (fig. 82, *p.bc.c.)* as well as with the

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anterior capsular cartilage. By this process of fusion the fenestra basicapsularis (figs. 81, 82, *f.bc.*) has formed. The posterior edge of the posterior basicapsular commissure extends caudally as a ridge (DE BEER's hypotic lamella) below the glossopharyngeal nerve past the point where this nerve has left the auditory capsule. In addition to the auditory cartilages mentioned, there is in this stage one more cartilage present enclosing ventrally the posterior semicircular canal and situated between this canal and the basicapsular cartilage. This cartilage, the cartilage of the posterior semicircular canal, or the cartilage of KÄLLBERG (fig. 81, *c.K.*), as I will call it, is already chondrifying or chondrified and lies close to the parachordals, from which it is, however, entirely separated. Its position is that of a posterior part of the processus dorsalis. It consists of a perpendicular lamella forming part of the wall of the brain case and a horizontal lamella extending below the lower limb of the posterior semicircular canal. The cartilage of KÄLLBERG in *Etmopterus* as in *Squalus* (where it was not described!) develops independent of the lateral edge of the parachordal plate in the lateral wall of the brain cavity. It later fuses with the parachordal. It forms posteriorly the posterior lower part of the auditory capsule (as will be explained in another part of this work). The lateral and posterior (dorsal) border of its horizontal lamella fuses with the posterior dorsal part of the auditory cartilage and helps form the glossopharyngeal canal.

The occipital column (figs. 81, 82, *o.c.*) has grown considerably. Its anterior margin rises abruptly dorso-frontad and forms, with the parachordal, an incisure for the vagus nerve. Over the caudal part of the column runs the first spinal nerve root. The basal lamellae of the cervical region now have segmentally arranged thickenings, in which chondrification has begun, resulting in the formation of basidorsals and basiventrals. These, by prochondrium, are connected with the occipital column and with each other. From the basal lamellae along the sides of the vertebral column denser blastematic lamellae have arisen between each two basidorsals. Above each basidorsal this blastematic part is pierced by the foramen for a ventral spinal root.

The angle between parachordal and polar cartilage + trabecula has straightened out considerably (fig. 81). The dorsal end of the polar cartilage (figs. 81—83, *p.b.*) reaches the caudal extension of the acrochordal tissue (figs. 81—83, *a.c.r.*), which covers the parachordal ventrally. The posterior part of the polar cartilage is extended transversally and shelflike below the jugular vein forming as in *Squalus* a basitrabecular process (fig. 83, *j.v.*). Between the medial borders of the two polar cartilages a blastematic commissure, the precarotid commissure (fig. 81), is seen running below the inner carotid artery. The anterior (lower) part of the polar cartilage is cylindrical with a notch for the efferent pseudobranchial artery (fig. 81) on its dorsal (anterior) edge. Frontally (ventrally) the polar cartilage is fused with the

posterior (dorsal) end of the trabecula. The trabecula (fig. 82. *trab.*) is spoonlike. It has a ventrocaudally directed rounded process against which rests the inside of the anterior end of the palatoquadrate (fig. 81). Frontally the trabecula is continued by a blastematic band (anterior sideplate; pretrabecular rod) (figs. 81, 82, *pr.r.*) lying dorsal to the medial part of the orbitonasal plate. On its frontal end is inserted the obliquus inferior muscle (fig. 81, *m.o.i.*). In front of this insertion point lies the (foramen of the) orbito-nasal vein (fig. 81, *o.n.v.*). The lamina orbitonasalis (figs. 81, 82, *l.o.n*) is a broad triangular blastematic lamella, medially connected with the anterior sideplate, extending laterally into the lower eyebrow, the mesenchyma of which seems to be the source for the lateral growth of the lamella in later stages of development. This lower eyebrow (fig. 81, *e. m.*) mesenchyma is continuous with the upper eyebrow mesenchyma, frontally, as well as caudally. This mesenchyma also extends frontad, sending out a process which borders the primary nasal capsule frontally and laterally. This frontal extension of the mesenchyma of the eyebrow area is very thick. Frontally its thick deeper part is well differentiated from its superficial part and it is partly separated from it by the etmoidal branch of the ophthalmicus superficialis VII. nerve. Caudally the two parts are not well differentiated from each other in the 30 mm stage, but there is a deep layer of rather dispersed cells present, caudally joining the orbitonasal lamina (figs. 81, 82, *l.o.n.*). In the 35 mm stage the deep part of the blastema is well separated

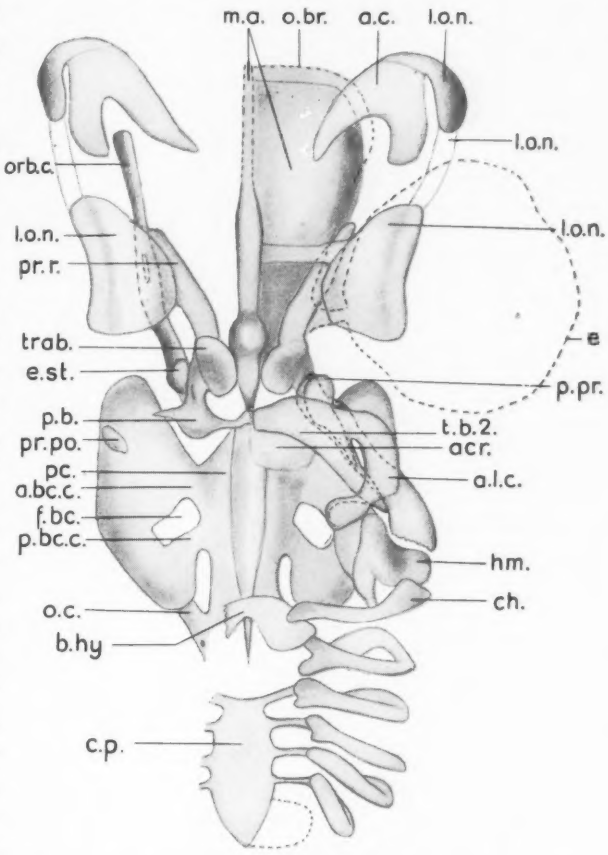

Fig. 82. *Etmopterus*. 30 mm. Skull. Reconstruction. Ventral aspect.

from the superficial also in its caudal part which is directly continuous with the orbitonasal lamina.

The chondrified part of the orbital cartilage (figs. 81, 82, *orb.c.*) forms a triangular, posteriorly short rodlike lamella, extending caudally towards the acrochordal tissue and joining it. This cartilage always keeps its connection, by means of a blastematic lamella, with the supraorbital mesenchyma. Dorsal to the trochlear nerve this lamella is chondrifying so that the nerve pierces the orbital cartilage trough an elongated slit-like fenestra (fig. 81, *IV.*) of which the borders are prochondrial. The orbital cartilage and the polar cartilage + trabecula are connected by a connective tissue membrane forming the medial wall of the orbita. This membrane (fig. 81) is about to chondrify posteriorly. The optic fenestra is very wide.

The eyestalk (figs. 81, 82, *e.st.*) is well defined and connected with the lateral part of the acrochordal tissue.

The medial area (fig. 82, *m. a.*) is superficially rather narrow, extending from the palatoquadrate symphysis posteriorly to the level of the frontal part of the nasal sacs anteriorly. The caudal part of the area as in *Squalus* enters between the trabeculae forming part of the brain envelop. At the level of the medium part of the lamina orbitonasalis, the deep part of the medial area is connected with the medial border of the lamina orbito-nasalis (fig. 82) and frontal to this connection it is connected with the anterior sideplate or pretrabecular rod (figs. 81, 82, *pr. r.*). Frontal to the side plate the deep part of the medial area is continuous with the membrane, forming the anterior part of the orbital wall. Thus the deep medial lamina covers at least part of the ventral surface of the brain. Frontally the lamina does not ascend on the lateral surface of the brain. Futhermore it is very diffuse.

The annular cartilage (figs. 81, 82, *a.c.*) of the nasal capsule is as in *Squalus* foreshadowed by a horseshoe-shaped blastema surrounding the nasal opening anteriorly.

The palatoquadrate and the mandibular portions of the mandibular arch are not yet separated but the locus of the future separation is well discernible. The palatoquadrate of *Etmopterus* is of very great interest, as stated by KÄLLBERG, and therefore will be described at some length. In the 25 mm stage the palatoquadrate consists of two parts viz. the palatoquadrate proper with its anterior tip, the future orbital process, in intimate contact with the lateral border of the trabecula, and the "teethblastema" which is in continuity with the blastema of the labial cartilages throughout almost its entire length. The "teethblastema" of the 30 mm stage has differentiated in a deeper portion (figs. 81, 83, *p.pr.*) and a more superficial (figs. 81—84, *t.b.z.*). The deeper portion of the blastema is condensed to a clubshaped body (figs. 81, 82), beginning with the thickened part anteriorly below the future orbital process and continuing, narrowing, gradually caudad at the ventro-medial border of

the palatoquadrate to end a little behind its mid. The remaining part of the "teethblastema" also contains frontally the matrix of the palatine process, and forms caudally the rudiment of the teeth mesenchyma which in the 30 mm stage is separated from the blastema of the labial cartilage (figs. 81, 82, 84, *a.l.c.*) except in front.

The hyoid arch, undivided in the preceding stage, is now divided into two well chondrified elements, the hyomandibula and the ceratohyal (figs. 81, 82, *ch.*) (*hyoid*). The anterior upper part of the hyomandibula has a frontal process extending frontad to the level of the posterior end of the anterior auditory cartilage. Behind the spiracular canal the hyomandibula is cylindrical, and bends down towards the ceratohyal. At the upper end of the hyomandibula lies a rather big oblong blastematic mass (fig. 81, *ph.hy.*), corresponding to the pharyngobranchial elements of the branchial arches. This mass extends caudally in a blastematic band which joins the epibranchial part of the first branchial arch. The frontal part of the hyomandibula is covered by an oblong blastema, ventrally connected with the mandibular arch near the point where the lower yaw articulation will be established, this *postspiracular* blastema will be considered

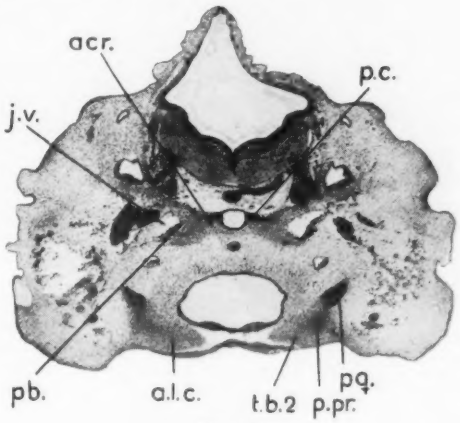

Fig. 83.

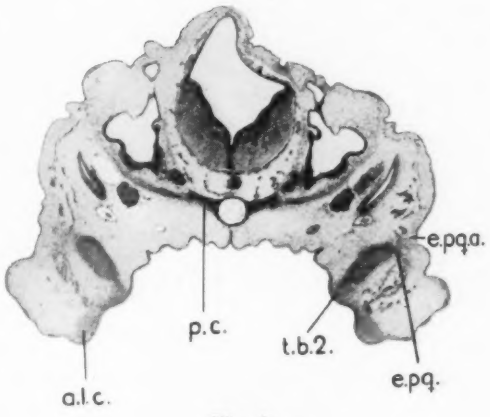

Fig. 84.

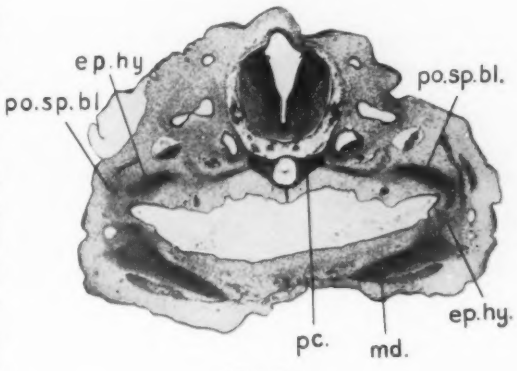

Fig. 85.

Figs. 83—85. *Etmopterus.* 30 mm. Transverse sections through the head region.

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later. A prespiracular blastema is also present. It is connected with the palatoquadrate portion of the mandibular arch anterior to the postspiracular blastema (figs. 81, 85, *po.sp.bl.*).

The branchial elements (figs. 81, 82), separate pieces in the preceding stage, have now fused in each arch to a dense prochondrium. The four anterior arches have their upper parts pierced by nerves to the musculus adductor branchialis. These foramina have, as VAN WIJHE demonstrated in *Squalus,* been formed as notches, which have later closed to foramina. This is clearly seen in a 27 mm stage. In the 30 mm stage no foramina are present in the ceratobranchial parts of the arches. The fifth arch is as in *Squalus.* No branchial rays are present.

The copular plate (fig. 82, *c.p.*) consists of an oblong blastematic lamella, in the midline extending from the region of the second branchial arch to the end of the branchial basket. In the 30 mm stages, as well as in that of 27 mm the copular lamella is unsegmented. The primary rudiment seems to grow frontally only. From the ceratobranchial parts of the second to the fifth arches slender blastematic strands extend mediad. These strands represent the hypobranchial elements of their arches. The lower tip of the first branchial arch lacks such a strand. On the other hand, there lies in the medial line between the hyoid arches a broad $\wedge$-shaped blastema the posterior legs of which are directed towards the first branchial arch. A blastematic part of the ceratohyal extends towards the angle of the $\wedge$. The $\wedge$-shaped blastema is the basihyal (fig. 82, *b.hy.*) of previous authors, but apparently represents the basihyal + the first basibranchial.

Etmopterus spinax, stage 34 mm.

In the otical region the parachordals have fused below the notochord by means of a very thin layer of cartilage. A similar layer on the dorsal side of the notochord is present in the region of the occipital column only. Nevertheless the notochord is surrounded by a thick layer of cartilage cells which, however, belongs to the external notochordal sheath where chondrification has taken place.

The two external rudiments of the auditory capsule, as in the preceding stage, have reached each other. The posterior part of the anterior cartilage, ventrolateral to the sacculus, has fused with the posterior cartilage. By this process in the floor of the capsule remains a wide fenestra representing a fenestra basicapsularis (fig. 87), bordered anteriorly by the commissura basicapsularis anterior, posteriorly by the commissura basicapsularis posterior. According to DE BEER (1931) the latter commissure does not exist in *Scyllium* at least. Thus the 34 mm stage behaves much as the 30 mm with regard to these characteristics.

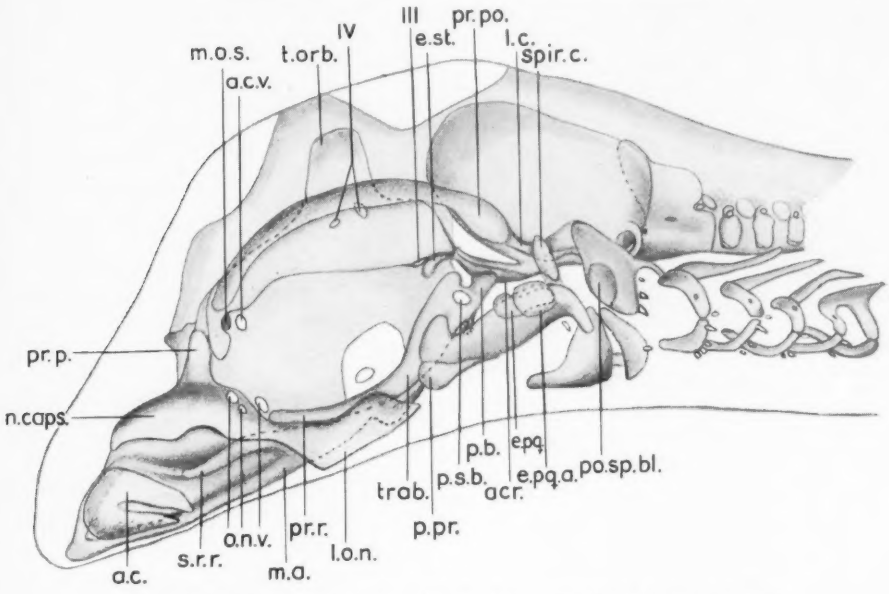

Fig. 86. *Etmopterus*. 34 mm. Skull. Reconstruction. Lateral aspect.

The chondrified part of the anterior cartilage of the otic capsule encloses the lower part of the anterior semicircular canal like a bowl, and at the anterior border of the sacculus its lateral part reaches the upper part of the lateral semicircular canal. Posteriorly it only reaches up a little on the outside of the sacculus, and after fusion with the posterior cartilage, the lateral wall lowers, forming a cartilage lamina, ventro-lateral to the glossopharyngeal nerve and an accompanying branch of the vena capitis lateralis. In the posterior part of the auditory organ the cartilage capsule is formed by the cartilage of the posterior semicircularly canal or cartilage of KÄLLBERG, established in the preceding stage. The cartilage of KÄLLBERG has grown considerably and has pushed away the primary cartilage rudiment. Its anterior guttershaped part has begun to fuse with the parachordal. Posteriorly the cartilage becomes more like a bowl. Somewhat anterior to the occipital column its medial wall meets that less chondrified cartilage which surrounds the upper part of the posterior semicircular canal, and from their meeting point a cartilaginous lamella enters horizontally between the upper and lower part of the canal, enclosing the canal in a tube. The medial, ventral and lateral walls of the tube are formed by the stronger chondrified cartilage of the posterior semicircular canal, whereas the dorsal wall is less chondrified, scarcely more than prochondrial, and derived from the lamella just mentioned which continues the lamellar system enclosing in this stage the other canals and also the dorsal part of the posterior semicircular canal. The lateral wall lies between the

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posterior semicircular canal and the nervus glossopharyngeus, forming the inner and also, by a flattened part, the dorsal wall of the glossopharyngeal canal. The lateral wall and the floor of this canal are formed by the posterior auditory cartilage. The glossopharyngeal nerve leaves the brain cavity at the anterior end of the cartilage of KÄLLBERG, between it and the processus dorsalis. It runs below the ventral part of the posterior semicircular canal, and thereafter, together with an acusticus branch, follows the lateral side of this canal, lying immediately dorsal to the low outer wall of the guttershaped part of the cartilage of KÄLLBERG. While further along caudally this wall rises dorsad and the said acusticus branch runs along its inside close to the semicircular canal, the glossopharyngeal nerve lies outside the cartilage and leaves the auditory capsule through the nerve canal described above. The posterior margin of the cartilage of KÄLLBERG rises dorsad. This cartilage thus forms the posterior pole of the auditory capsule. It extends far behind the posterior basicapsular commissure. The processus dorsalis has fused frontally with that medial wall portion partly formed in the preceding stage by the anterior capsule cartilage. By this process a foramen for the auditory nerve has been established. The nervus vagus leaves the brain cavity between the cartilage of KÄLLBERG and the occipital column through the incisure at the base of the latter.

The occipital column has grown frontally to embrace the occipital nerve Y. The first ventral spinal nerve root is now enclosed in an incisure (fig. 86). The vertebral centers (fig. 86) are well chondrified. The vertebral arches rise and enclose at least the next two ventral spinal roots. Intercalars have originated from the thickened parts of the blastematic sheath around the notochord. Only the first intercalar has condrified, the others as yet are prochondrial.

The angle between the trabecula and the parachordal is decreasing (fig. 86). The posterior process of the trabecula is less marked. The orbital process of the palatoquadrate is in contact with the outside of the trabecula. The angle between the trabecula and the anterior sideplate or pretrabecular rod (figs. 86, 87, *pr.r.*) is also less pronounced. The sideplate, has grown longer than in the preceding stage.

The polar cartilage and the trabecula are now connected dorsal as well as ventral to the efferent pseudobranchial artery (fig. 86, *p.s.b.*), this artery thus being enclosed in a foramen. This enclosing process depends upon chondrification of the ventral part of the membrane in preceding stages connecting the trabecular system with the orbital cartilage. Beginning chondrification of this membrane between the pituitary vein and the oculomotor nerve is about to establish the "posterior sideplate" of MORI. The polar cartilages, now quite chondrified, have fused with the subchordal part of the acrochordal tissue. They are also connected with each other by two commissures, the

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postpituitary and the precarotid commissure, of which the former is fused to the lower surface of the acrochordal tissue (*a.c.r.*). Anterior to the postpituitary commissures (fig. 87, *pp.c.*) runs the hypophysial vein (v. pituitaria) (connecting the two orbital sinuses) and rostral to the vein the rudiment of the "posterior sideplates" rises forming an incisure caudal to the foramen of the efferent pseudobranchial artery. The precarotid commissure establishes the posterior border of the hypophysial fenestra. The anterior margin of the fenestra is in this stage indicated by broad medial processes (fig. 87, *trab.*) of the trabeculae approching each other in the midline anterior to the hypophysis. Anterior to this point the trabeculae run parallel. The anterior sideplate (fig. 86, 87, *pr. r.*) is connected with the very broad and largely blastematic lamina orbitonasalis. This lamina consist of a caudally, frontally and laterally expanded plate, the "antorbital process" of earlier writers. Frontally the lamina orbitonasalis continues in a narrower portion (in preceding stages diffusely outlined) forming the anteroventral part of the frame of the orbit (figs. 86, 87). This part is partly penetrated by the orbitonasal veins (*o.n.v.*) (three are present in the actual specimen). In front of this frame portion there follows without line of demarcation, the rudiment of the lateral cartilage of the nasal capsule.

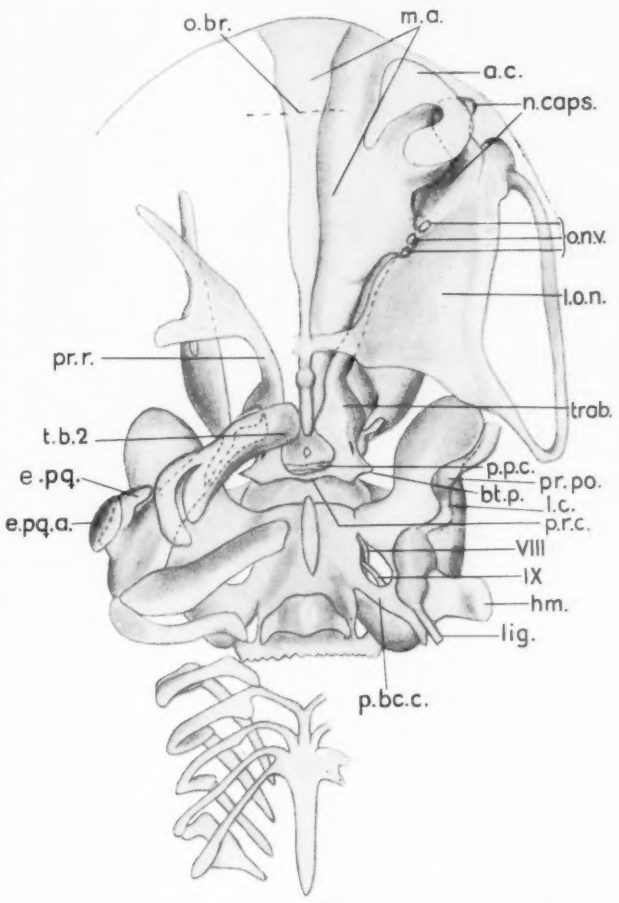

Fig. 87. *Etmopterus*. 34 mm. Skull. Reconstruction. Ventral aspect.

As in *Squalus* the deep part of the medial area (figs. 86, 87, *m.a.*) enters between the trabeculae and dorsal to them broadens to form a bed upon which the brain rests. Thus the trabeculae are connected with each other by

a part of the medial area. The superficial part of this area forms a keel ("medial rod") on the lower surface of the "trabecular plate" and passes over frontally into the rostral plate or rostrum. In this stage the "rostrum" is quite mesenchymatic, consisting of the deep part of the medial area of the anterior head region. There it embraces the brain cavity ventrolaterally. Frontal to the brain it forms the rudiment of the walls of the cavum precerebrale.

The posteromedial border of the lamina orbitonasalis is connected with the medial area ("medial rod") (fig. 87).

The "medial rod" as seen from below extends from the fenestra hypophyseos to the anterior tip of the head. Its posterior part is not in contact with the epithelium of the skin and is formed by a medium portion of the medial area. Its anterior division lies in contact with the epithelium and consists of the superficial as well as the medium part of the area. The anterior part in addition is broader and less developed as to chondrification than the posterior which is about to chondrify. Level with the parallel part of the trabeculae the rod has a spherical thickening (fig. 87). Seen from the lateral side the medial rod has a bandlike aspect, (fig. 86). As already mentioned the upper border of this band enters between the trabeculae and broadens (deep portion of the medial area) to become the membranous bed for the brain inside the trabeculae. Frontally, anterior to the lamina orbitonasalis, the rostral band has a thickened upper border lying on the midline below the brain. This thickened border may be called the "suprarostral rod" (fig. 86, *s.r.r.*)

The orbital cartilage is independent as in the preceding stage. It has grown considerably in front, and from its upper border a medially directed chondrifying lamella is forming as the first rudiment of the cranial roof, the tectum orbitale (fig. 86, *t.orb.*). There are two trochlearis foramina in the reconstructed specimen, in others there is only one. A notch in the lower border of the orbital plate near its posterior corner contains the oculomotor nerve.

At the frontal end of the orbital cartilage the rudiment of the preorbital cartilage (fig. 86, *pr.p.*) is seen. It is fused to the lower part of the orbital frame. The ophthalmicus superficialis nerve passes between the rudiment and the supraorbital crest (fig. 86) which is developing in this stage. The supraorbital crest, as well as the preorbital cartilage, are developing from the eyebrow area. Caudally the crest continues upon the anterior part of the auditory capsule where it is fused with the *primary* postorbital process (figs. 86, 87, *pr.po.*) as in *Squalus* forming a *secondary* postorbital process. The eyebrow contains a mesenchymatic mass which forms a ring round the eye (in the upper and lower eyebrow). The lower eyebrow mesenchyma is continuous with the lateral border of the orbitonasal plate blastema. Anteriorly the eyebrow ring has a rather bulky frontal process. This process later fuses

with the lateral cartilage of the nasal capsule (figs. 86, 87, *n.caps.*), forming the lateral wall of the ethmoid canal (of GEGENBAUR).

A membranous rudiment of the epiphysial bridge is present. The medial orbital wall is of membrane. A rather big fenestra optica is present.

In the mandibular arch the patatoquadrate has separated from the mandibular portion. In the palatoquadrate as described in the preceding stage, two more elements are now sufficiently differentiated as to be distinctly outlined. The posterior of these rudiments is the rudiment of the prespiracular cartilages (fig. 86, *spir. c.*) (mandibular branchial rays), connected with the postorbital process by means of a "lateral commissur". The anterior must be considered an hitherto unknown element of the selachian skull. It is an oblong blastem-

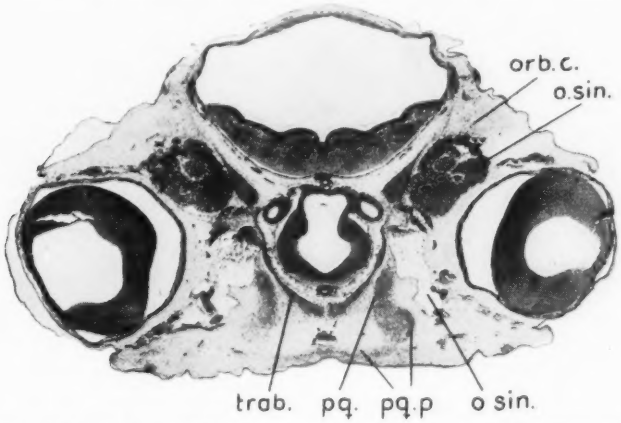

Fig. 88. *Etmopterus.* 34 mm. Transverse section of the trabecular region of the head.

atic mass of cells, the "extrapalatoquadrate" (figs. 86, 87, *e.pq.*), developing from a small subepidermal area (extrapalatoquadrate area) (*e. pq.a.*) situated antero-ventral to the spiracle and immediately outside the frontal end of the posterior half of the palatoquadrate. From this area cells are sinking towards the upper border of the palatoquadrate, as is already seen in the 30 mm stage (fig. 84, *e.pq.* resp. *e.pq.a.*). A small distance from this border an oblong mass forms in this way. On this blastema there insert constrictor muscle fibres which constitute the musculus levator palatoquadrati and the m. adductor mandibulae. These muscles do not thus primarily insert upon the palatoquadrate proper but upon this independent rudiment. Later as the rudiment fuses with the border of the palatoquadrate the muscles become inserted upon a muscular process (otic process) of this cartilage. The morphological and phylogenetical bearings of these observations will be treated with further on.

Thus in this stage of development the mandibular arch of *Etmopterus* consists of the following elements: 1) The palatine part (fig. 88, *pq.p.*), 2) the

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toothplates, 3) the labial cartilage, 4) the symphysial blastema of the palatoquadrate, 5) the palatoquadrate proper (*pq.*) with the orbital process, 6) the muscular process (otical process) of the palatoquadrate, 7) the prespiracular and postspiracular (fused with the hyomandibular) cartilages, 8) the lateral commissure, 9) the meckelian cartilage and 10) the mandibular symphysial blastema.

The hyoid arch appears essentially as in the preceding stage, but along its posterior margin a number of independent rudiments of hyoid rays has formed (fig. 86). The hyomandibula carries three, of which the most ventral is the longest, and the ceratohyal only one. In the 27 mm stage no rays are present on the hyoid arch.

The anterior part of the pharyngohyal portion is as in the preceding stages, its posterior portion is now incorporated with the hyomandibula, forming its upper part and the ligament connecting it with the first epibranchial. At the lower anterior part of the hyomandibula a disc of prochondrial tissue the "postspiracular cartilage", staining differently from that of the medium part of the hyomandibula, is distinctly seen. On this disc (fig. 86, *po. sp.bl.*) the levator muscle of the hyomandibula (part of the constrictor dorsalis) is inserted. The morphological importance of this disc will be discussed in another part of this work.

Between the secondary postorbital process and the anterior border of the pharyngohyal there is present a blastematic bridge, which passes lateral to the jugular vein and the hyomandibular nerve (of *VII.*). This bridge is the rudiment of the lateral commissure (figs. 86, 87, *l.c.*) of DE BEER. It has in this stage only a very diffuse connection with the rudiment of the prespiracular cartilages.

The branchial arches (figs. 86, 87) are chondrified, the chondrification having been carried on from three different centres, corresponding to the three original rudiments. The arches, continuous in the preceding stage, are thus again divided into a pharyngo-, an epi- and a ceratobranchial. The hypobranchial 2—5, still prochondrial, reach the anterior broader part of the copular plate. The first ceratobranchial has a short frontally extending process. Its medial portion is extended in caudo-medial direction. The latter corresponds to a short process on the ceratobranchials 2 and 3. A similar process is also present on the ceratohyal. The "basihyal" consists of a broad transversal plate. The medial part of the plate is thicker than the lateral parts, which run out caudally in short horns.

The branchial rays are about to be formed. They form separately as the hyoid rays, decreasing in number caudad. The upper ceratobranchial rays are differentiated at first, the epibranchial rays come later.

Etmopterus spinax, stage 36 mm.

This stage differs in the otical region from the preceding in some details. The chondrified part of the lateral wall of the auditory capsule now extends dorsally up around the lateral semicircular canal, above and below which inwardly directed crestshaped thickenings have arisen, enbedding the canal in a groove. At the medium part of the capsule the groove is closed, forming a canal. The lateral wall of the anterior part of the capsule is still low. Therefore the anterior semicircular canal is here visible from the lateral side. From the medial wall of this region a cartilaginous ridge has protruded between the upper and lower part of the same canal. This ridge is visible from the lateral side through the incomplete lateral wall. It passes as a bridge from the inner to the outer wall on the inside of which it runs caudad as the upper delimiting ridge of the lateral semicircular canal. Behind the anterior gap the lateral wall of the capsule rises dorsad to form the still incomplete cartilaginous roof of the capsule dorsal to the lateral semicircular canal. From this roof a blastematic plate extends over the brain, establishing the first rudiment of the tectum synoticum. This tectum is forming in the membrane already covering the brain dorsally in the preceding stage. Posteriorly the lateral wall of the auditory capsule is continuous, not only with the posterior basicapsular part of the auditory capsule, but also with the lateral part of the cartilage of KÄLLBERG. This latter connection is established by a prochordrial gutter formed dorsally around the lateral semicircular canal. This gutter is separated from the posterior basicapsular cartilage by a fissure filled in with a sparse blastema. The cartilage of the posterior semicircular canal (cartilage of KÄLLBERG) forms the caudal part of the auditory capsule. The posterior part of the capsule is thus formed by the primary independent cartilage of KÄLLBERG, whereas the posterior basicapsular cartilage in this region merely forms the lateral wall of the glossopharyngeal canal.

The fenestra basicapsularis is still present in the floor of the capsule. The medial wall is complete only in the anterior and posterior parts of the capsule. The processus dorsalis, however, has grown backwards and encloses a small vein in a foramen. The processus has fused caudally with the cartilage of KÄLLBERG, dorsal to the glossopharyngeal nerve which thus runs from the brain cavity into the auditory capsule through a foramen of its inner wall. The upper part of the occipital column leans against the medial wall of the auditory capsule.

The incisure for the pituitary vein is now closed to a foramen, the entrance to the interorbital canal. The closure of the notch has been effected by a cartilaginous connection between the polar cartilage and the pila antotica. This connection KÄLLBERG called the pila praepituitaria. The pituitary vein is not yet surrounded by cartilage during its passage through the cranial cavity.

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The orbital cartilage still has no connection with the parachordal. The orbital membrane is preparing for chondrification dorsally and forms a prochondrial lamella.

To this stage of development the following remarks may be added. The anterior process of the eyebrow mesenchyma has joined the posterior part of the rudiment of the lateral cartilage of the nasal capsule, forming the lateral wall of the ethmoid canal. The optic fenestra has decreased considerably. The anterior tip of the notochord is bent backwards so strongly that the tip portion lies in close contact with the portion next to the tip. The subchordal part of the acrochordal tissue is about to chondrify and thereby fuse with the parachordals.

Etmopterus spinax, stage 43 mm.

Between this stage and the preceding there is a gap in the series. The development of the skull, however, has not proceeded too far as to prevent an interpretation based upon the preceding stages. In reality the skull is already so well outlined in the 34 mm stage, that it is even possible in some cases to determine adult structures. In addition demarcation lines where fusions have taken place are still present in the 43 mm stage, thus facilitating the interpretation.

The notochord is decreasing in thickness anteriorly. Its hook is still present. The notochord is now enclosed by cartilage in the same manner as in *Squalus.* In the caudal parts of the skull the boundaries between the cartilage of the external notochordal layer and the parachordals are disappearing. In the occipital region a thin cartilage layer is also present on the dorsal surface of the degenerating notochord.

The auditory capsules anterior to the ductus endolymphaticus are connected with each other by the well developed tectum synoticum (fig. 91, *t.syn.*). The earlier developed rudiment of the orbital tectum (figs. 89, 91, *t.orb.*) has not developed further, and is still represented by two prochondrial processes. On the anterior part of the orbital cartilages there is on each side a similar process, the rudiment of the cartilaginous epiphysial bridge (figs. 89—91, *ep.br.*).

The lateral semicircular canal is now separated from the other parts of the labyrinth by a thick mass of cartilage, connected with the lateral wall, but it is separated from the lateral surface of the capsule only by a thin cartilage layer. The auditory capsule has got a complete cartilaginous roof by means of chondrification of the prochondrial or blastematic rudiment. The posterior part of the tectum synoticum is not only connected with the external wall of the capsule, but also with the inner wall which is joined with the roof of the capsule medial to the anterior semicircular canal. This roof behind the tectum synoticum is open to admit the ductus endolymphaticus and

therefore loses its connection with the medial wall, while this wall rises between the brain and the ductus endolymphaticus, enlarging the tectum caudally. Behind the endolymphatic duct, where the posterior semicircular canal issues from the utriculus, the medial wall decreases considerably in height. In this region the roof rudiment is narrower. Further along caudally the medial wall rises again and joins the lateral wall below the upper part of the posterior semicircular canal. Somewhat further along caudally a connection is effected, also medial to the canal. The fenestra basicapsularis has disappeared but a thin portion of the floor of the capsule indicates its former position. The cartilage of the posterior semicircular canal (cartilage of KÄLLBERG) has fused with the parachordal and with the posterior basicapsular cartilage. In

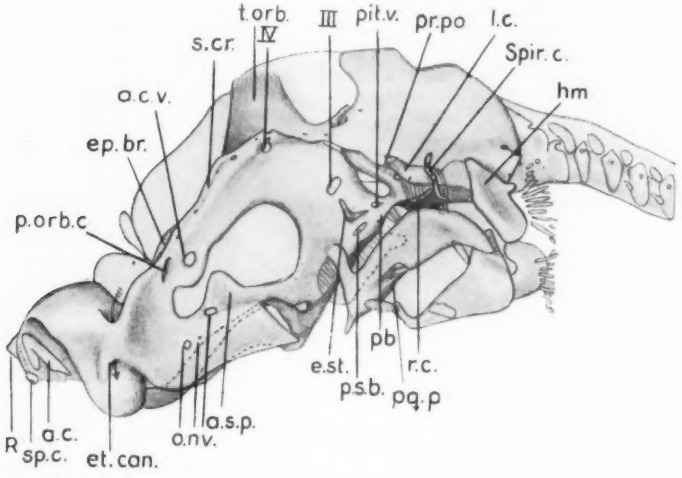

Fig. 89. *Etmopterus*. 43 mm. Skull. Reconstruction. Lateral aspect.

section the floor of the capsule below the posterior canal consits of two layers, a superior originating from the cartilage of KÄLLBERG and an inferior from the posterior basicapsular cartilage. Below the lagena and the glossopharyngeal nerve it consists of the posterior basicapsular cartilage alone. The glossopharyngeus canal is now fully developed. This was effected by fusion of the lateral border of the posterior basicapsular cartilage with the lateral wall of the auditory capsule. Caudally this line of fusion is seen as a slit through which runs a small glossopharyngeal nerve fibre (fig. 89). A little part of the tip of the lagena enters the nerve canal. On the lateral surface of the auditory cartilage two ridges have arisen the dorsal of which apparently belongs to the posterior basicapsular cartilage, whereas the ventral seems to be a descendant from the "pharyngohyal" rudiment. Between these ridges is situated the articular surface for the hyomandibula. Some details in regard to the auditory capsule will be described separately. The occipital

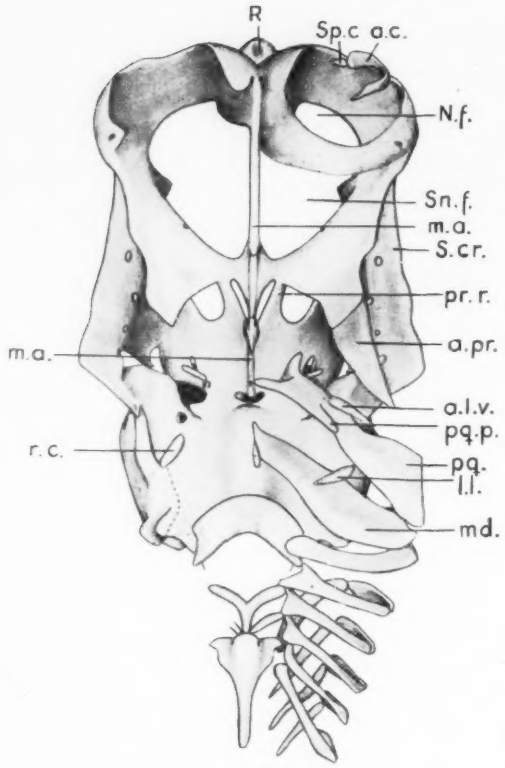

Fig. 90.

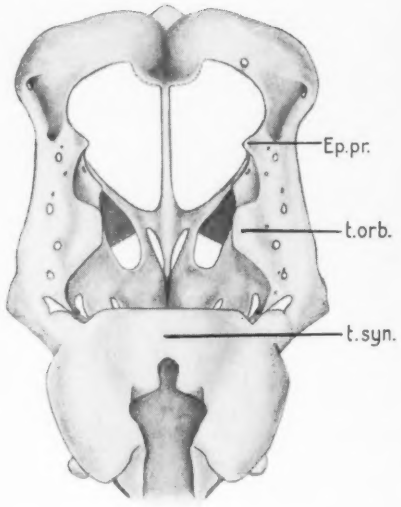

Fig. 91.

Fig. 90. *Etmopterus*. 43 mm. Skull. Reconstruction. Ventral aspect.

Fig. 91. *Etmopterus*. 43 mm. Skull. Reconstruction. Dorsal aspect.

column is about to fuse with the inner wall of the auditory capsule dorsal to the vagus nerve. The vena cerebralis posterior runs through the vagus canal. Vertebral basidorsals and intercalars (fig. 89) are now well chondrified. The ventral spinal roots pierce the basidorsals, the corresponding dorsal roots run anterior to the next intercalar. That part of the occipital arch, above which goes the first spinal root, is apparently a vertebra fused with the occipital column. Anterior and superior to this, notches and limiting lines in the cartilage suggest that an intercalar also is here attached to the skull.

The trabeculae are now joined on the medial line by means of the medial area (figs. 89, 90, 92, 93, *m.a.*) which enters between the trabeculae, forming a very narrow "trabecular commissure". In the polar fenestra the hypophysial foramen is separated from the inner carotid foramen by the praecarotid commissure on the middle of which the most posterior deep part of the medial area forms a medial area cartilage nucleus. As in the preceding stage the deeper layer of the medial area enters between the trabeculae and broadens dorsal to them to a bed (fig. 92, *m.a.*) supporting the brain. Towards that point where the trabeculae connect with the antorbital frame the medial

area becomes keelshaped, forming that big medial angle on the ventral side of the neural cranium (fig. 89) characteristic of the *Etmopterus* skull. In this region the trabeculae are degenerating along the medial keel and the bed of the brain is chondrifying, repairing the loss of cartilage of the trabeculae. At the tip of the (medial) angle the superficial part of the medial area seen from below is present as an oblong body (fig. 90) of prochondrial tissue. Anterior to this angle the medial keel again sinks down level the anterior sideplates or pretrabecular rods (fig. 90, *pr. r.*), but frontally again soon becomes keel-or ribbonshaped to continue as a medial keel forming the high internasal wall in the region of the nasal capsules. In front of the nasal capsules the medial area widens to a short conical rostrum still blastematic in composition (figs. 89, 90, *R.*).

Between the diverging borders of the antorbital frame (pretrabecular rods) which anteriorly continue the trabecula and the medial keel cartilage there exist fissures which have, however, been anteriorly shrunken to small openings by cartilage connections arising between the pretrabecular rods and the medial rod (fig. 90). The connection between the lamina orbitonasalis and the medial rod, described in the preceding stage, forms the poste-

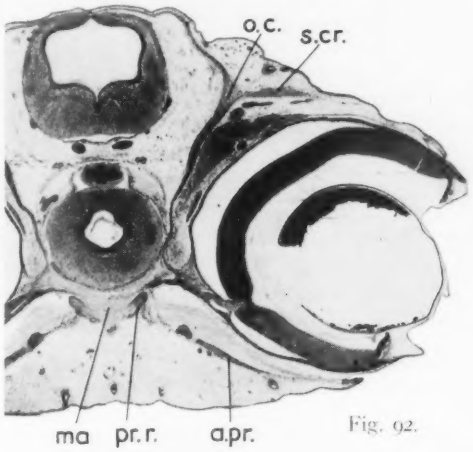

Fig. 92.

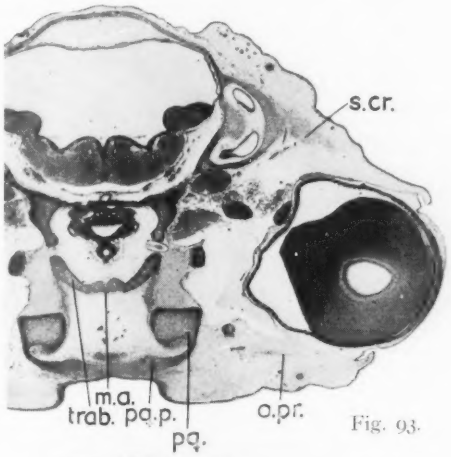

Fig. 93.

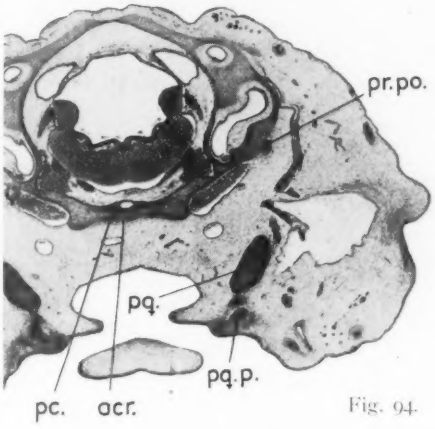

Fig. 94.

Figs. 92—94. *Etmopterus*. 43 mm. Transverse sections of the head region.

rior border of the nasal (fig. 90, *N.f.*) + subnasal (fig. 90, *Sn.f.*) ("basal communication") fenestra.

The postpituitary commissure has chondrified and is now almost completely fused with the posterior part of the acrochordal tissue, now chondrified, which underlies the parachordals, of which the preauditory part is but feebly developed (fig. 94,*pc.*) as in the preceding stages.

The trabeculae are connected with the orbital cartilages by the posterior "sideplates" (fig. 89). These run parallel to the pila antotica and anterior to them. The foramen of the oculomotor nerve is a remaining part of the primary fenestra between the pila and the sideplates.

The "anterior sideplate" (fig. 89, *a.s.p.*) is broadening through chondrification of the membranous medial orbital wall between the opticus and the orbitonasal canal. The orbitonasal lamina laterally has a thin blastematic border portion which extends to the mesenchyma of the lower eyebrow. Caudally this border is detached from the eyebrow and continues caudad as a long pointed triangular lamina connected with the posterior border of the chondrified part of the orbitonasal plate. As in *Squalus* this triangular lamina represents the "antorbital cartilage" (figs. 90, 92, 93, *a.pr.*) or "Flossenstützknorpel" in rays. It is pierced at its base by buccalis fibres and small arteries.

The orbital cartilage is connected posteriorly by a "taenia marginalis" with the auditory capsule. This "taenia marginalis" consists of two parts. The one is formed by chondrification of that membrane which in preceding stages continues the orbital cartilage caudad dorsal to the facialis and trigeminus nerve roots. This membrane continues caudally in the wall of the brain case with which the auditory capsule is connected. The actual chondrified part of this membrane forms in part a cartilage tongue at the dorsal margin, and in part of a similar tongue at the ventral margin of the anterior part of the auditory capsule. The other part is formed by the supraorbital crest (figs. 89, 90, 92, 93, *s.cr.*) cartilage which continues caudally upon the lateral surface of the auditory capsule where it ends in connection with, and partly covering, the primary postorbital process. Between the two parts of the "taenia marginalis" run fine bloodvessels and small branches of the ophthalmicus superficialis VII, and between the otical part of the supraorbital crest and the postorbital process respectively runs an otical branch of the lateralis system. As the lateral wall of the auditory capsule medial to the postorbital process is not wholly complete, the said nerve seems to enter the auditory capsule. In front the orbital cartilage connects with the lamina orbitonasalis, and the supraorbital crest fuses with the praeorbital cartilage or crest. This region of the skull has become established, as in *Squalus*, by means of a relatively independent praeorbital cartilage. The ophthalmicus profundus nerve follows a course different to that in *Squalus*. It enters the praeorbital canal (fig. 89, *p.orb.c.*) together with the ramus ophthalmicus superficialis VII.

From the anterior part of the optic fenestra a foramen corresponding to the profundus foramen in *Squalus,* is formed. It lies anterior to the "anterior sideplate". In *Etmopterus* this foramen later closes entirely. The foramina of the vena cerebralis anterior (*a.c.v.*) and venae orbitonasales (*o.n.v.*) (there are two or three present) are formed as in *Squalus.*

The development of the primary lateral cartilage of the nasal capsule was described in the preceding stage. In the 43 mm stage the nasal capsule has got new elements added through independently formed blastematic membranes encircling the nasal sac anteriorly, medially, laterally, and caudally (fig. 89, 90). The anterior lamina is attached at the lateral border of the deep lateral extension of the internasal septum. Laterally this lamina is continuous with a similar but narrower lamina attached to the ventral edge of the primary lateral cartilage of the nasal capsule. The medial lamina is attached to the ventral border of the internasal septum. As the internasal septum decreases in height caudally the lamina bends laterally, forming the posterior wall of the nasal capsule and laterally joining the lateral lamina (fig. 90). Through the development of these capsular elements the big nasal + subnasal fenestra has been divided into the anterior nasal fenestra (*N.f.*) and the posterior subnasal (*Sn.f.*) (basal communication of GEGENBAUR). That process, of the lower eye-brow area, in the 30 and 34 mm stages extending frontad from the circumocular ring, is joined with the primary lateral cartilage of the nasal capsule, and forms the lateral wall of the ethmoid canal (fig. 89, *et.can.*), and helps support the secondary capsular lamina (fig. 89). Two nasal cartilages are present at the opening of the nasal sac; the first, horseshoeshaped and derived from the primary nasal capsule rudiment, corresponds to the "Ringknorpel" of MORI or annular cartilage. The second and smaller, situated medial to the former, corresponds to MORI's "Spangenknorpel" (figs. 89, 90, *sp.c.*).

The upper as well as the lower jaws respectively meet on the medial line, forming symphyses (fig. 90). In the posterior part of the symphysis of the lower jaw two prochondrial centers lie side by side. The symphysial tissue of the palatoquadrate is well developed and seems to be divided into two lateral parts or at least to have lateral processes in front of the palatine process. See next stage! The palatoquadrate as in *Squalus* is connected by means of a membrane with the trabecular part of the cranial base. The palatine part of the palatoquadrate is well separated from the rest of this part and has a rodlike prolongation lying immediately below the inferior margin of it (figs. 89, 90, *pq.p.*). This prolongation is connected with the palatoquadrate proper only by a thin chondrified layer. Caudally this layer is blastematic and disappears towards the end of the prolongation which is itself free. Through a foramen at its posterior part it is pierced by a branch of the orbital artery. The teeth blastema lies principally in the

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palatine part but continues caudally on the edge of the palatoquadrate proper. That posterior element (the extrapalatoquadrate) lying external to the palatoquadrate, described in the 30 and 34 mm stages, has fused in the 43 mm stage with the lateral border of the palatoquadrate there forming a strong muscular process upon which the muscles insert. This process later grows much bigger and then is already seen to represent the "processus oticus", homologous with the "olic process" in *Heptanchus*.

One praespiracular skeletal element is chondrifying. At its upper end, however, there is a series of small prochondrial pieces lying inside and somewhat dorsal to each other, forming a row of praespiracular elements (fig. 89, *Spir.c.*) (branchial rays).

That outjutting shelflike part of the polar cartilage, described in *Squalus* as the basitrabecular process, is continued caudally by a ridge on the ventrolateral surface of the auditory capsule. Ouside this ridge lies a separate rodlike cartilage (figs. 89, 90, *n. c.*), probably belonging to the praespiracular system of cartilages. The origin of this cartilage could not be discerned in *Etmopterus*, but in *Squalus* it was suggested to be a branchial ray belonging to the praespiracular complex.

A membranous lateral commissure is present between the postorbital process and the anterior end of the hyomandibular facet. This commissure is connected by an indistinct mesenchymtic lamella with the palatoquadrate.

An upper and a lower anterior lip-cartilage are chondrifying outside the mandibular arch.

The hyoid arch now carries a great number of rays (fig. 89), the biggest of which are the most ventral on the hyomandibula and the most dorsal on the ceratohyal. These almost face one another. None of the rays reach the hyomandibula, but the ceratohyal rays reach the ceratohyal. Some of the rays are cleft apically—a result of small secondary ray rudiments joining the primary rays.

The fate of the pharyngohyal element is not quite clear. Its anterior part is preserved as a mesenchymatic layer upon the lateral side of the auditory capsule. Its anterior end merges into the connective tissue rudiment of the "lateral commissure", the posterior section, has in part joined the hyoid arch forming the upper end of the hyomandibula, and in part is preserved in connection with the auditory capsule there forming the ridge bordering ventrally the articular facet for the hyomandibula. It could not be determined whether the facet also is covered with tissue derived from the pharyngohyal.

Furthermore the ventral parts of the branchial arches have chondrified. The copular plate by this process is now differentiated from the arches. A V-shaped element is articulated against the anterior margin of the copular plate (fig. 90). This element carries a rodlike cartilage on each side near its posterior end. The former consists of the hypobranchials of the second, the latter

that of the third arch. The hypobranchial of the fourth arch is incorporated with the copular plate. Its inner boundary is well discernable toward the medial rodlike part of the copular plate. The fifth hypobranchial is missing or incorporated without a boundary line with the copula. GEGENBAUR considered the V-shaped cartilage to be the hypobranchial of the first arch. The development, however, shows that this was an error. There is no articulation between the caudal process of the first ceratobranchial and the hypobranchial 2. If there would be any hypobranchial 1, it must be sought for anterior to the anterior angle of the ceratobranchial 1. In this stage this angle attains the posterior horn of the "basihyal" and articulates against it. These facts give evidence for the assumption that the "basihyal" is established by the two fused hypobranchials 1. RABINERSON (1925) has demonstrated that this is the case with rays and it is probably also the case with sharks. The fact that the ceratohyal articulates against the *ventral* surface of the "basihyal" supports this interpretation. In the branchial skeleton there exists no articulation between the ceratobranchials and the hypobranchials of the next arch, but the former is provided with a caudad directed process, extending below the hypobranchial of the following arch. If we assume that there were a secondary articulation between these elements it should lie on the ventral surface of the hypobranchial.

The branchial rays do not in general reach the arches. The upper ceratobranchial and the lower epibranchial rays display a tendency of fusing.

Etmopterus spinax, stage 55 mm.

The notochord is degenerating in its entire cranial extension. The part of the tiphook facing back is reduced to a hairfine thread (fig. 98). The boundary lines between the external sheath of the notochord and the parachordal cartilage are disappearing. Thus the notochord is embedded in cartilage throughout the entire otical region. Frontal to this part the notochord, flanked by the anterior parts of the parachordals, rests upon a big cartilage, apparently consisting of the posterior part of the acrochordal tissue. The tip portion of the parachordals is degenerating together with the tip of the notochord. This degeneration already commenced in the 43 mm stage.

The skull is about to assume its adult shape. Its roof, however, is not yet complete. The tectum synoticum (fig. 97, *t.syn.*) has enlarged considerably frontally as well as caudally. Anterior to it the orbital (*t.orb.*) and the epifysial bridges (*ep.br*) are established over the dorsal side of the brain. The anterior of these, forming the posterior border of the praefrontal fontanella, corresponds to the epiphysial bridge of other fishes. It extends transversely over the epiphysis, which is embedded in a pit on its lower surface. According to HARRISON in a certain stage of development of *Squalus* the epiphysis is enclosed in a pineal foramen. In 45 and 47 mm

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stages of *Etmopterus* the chondrification process, commencing the formation of the epiphyseal bridge laterally, extends more and more toward the dorsal midline and the epiphysis. In a 53 mm stage a new independent cartilage has formed on each side of the epiphysis. That on one side in this specimen is already connected by a slender thread with the (orbital) epiphysial process, that on the other, however, is still independent. These two cartilages form the cartilage surrounding the epiphysis. The formation of the bridge thus completely corresponds to that of the epifysial bridge in *Lepidosteus* and in principle also to that of *Amia*.

From the posterior margin of the tectum synoticum a medial process—a taenia medialis (fig. 97, *taen.med.*)—has grown backwards and joined a prochondrial bridge (fig. 97, *t.occ.*) (tectum posterius or occipitale) connecting in this stage the upper and anterior parts of the occipital columns. These parts are connected with the auditory capsules. In a 53 mm stage the taenia medialis does not attain the tectum posterius, which is already prochondrially established. A posterior fontanella, described by HARRISON in *Squalus*, was not found in *Etmopterus*. The taenia medialis and the tectum posterius chondrify simultaneously.

The taenia medialis forms the floor of the fossa parietalis (fig. 97). Behind the ductus endolymphaticus a thin cartilage bridge has joined the roof of the auditory capsule with its inner wall, giving rise to the foramen endolymphaticum. Caudal to this foramen opens the posterior canal vacuity of DE BEER (1931). In this the posterior semicircular canal is visible in the lateral part of the fossa parietalis, partly covered dorsally by cartilage substance. In the auditory capsules no considerable changes have taken place. The frontad running branch of the auditory nerve, immediately after its separation from the main nerve, was enclosed in the lateral wall of the auditory capsule.

The vagus canal (fig. 98, *X.*), as a result of the caudal growth of the auditory capsule, runs obliquely caudad and laterad. The occipital nerve *Y.* enters the canal (fig. 98, *y.*). From the occipital column ridges have developed dorsal and ventral to the vagus nerve, which thus runs in a groove on the outside of the column. The dorsal spinal nerves now pierce the anterior parts of the intercalars.

The angle between the parachordals and the posterior parts of the trabeculae has almost disappeared (fig. 98). In this region one finds, as a remainder of the earlier bend, a depression in the cranial floor, wherein rests the hypophysis, i.e. a fossa pituitaria (fig. 98, *f.pit.*). This fossa is anteriorly delimited by a thickened part which was formed, when the angle between the trabeculae and the medial keel cartilage (medial area) was filled in with cartilage, produced from the latter. The posterior boundary of the fossa, the dorsum sellae, as in *Squalus* is formed by the chondrified acrochordal tissue.

At the point, where the medial keel has its greatest height, it forms the "keel-cartilage" (figs. 95, 96, 98).

The ramus profundus (fig. 95, *prof.*) is now separated from the ramus ophtalmicus superficialis and pierces the preorbital crest somewhat anterior and ventral to the latter.

The nasal capsule has enlarged. In the preceding stage a membranous nasal capsule was formed. In this membrane chondrification has now taken place, and the figures (figs. 95, 96) give an idea of the extension of the chondrifying parts. With this lamella the "Spangenknorpel" has fused to

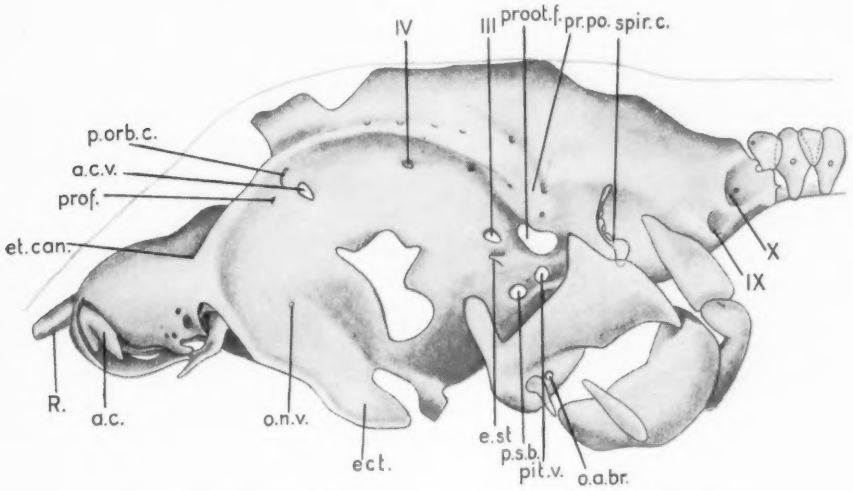

Fig. 95. *Etmopterus*. 55 mm. Skull. Reconstruction. Lateral aspect.

form the anterior nasal wall. The primary nasal + subnasal fenestra, as in the preceding stage, is divided into the definite fenestra nasalis, and the subnasal fenestra (ectethmoid fossa of ALLIS).

The anterior position of the nasal capsules seems to have caused the position of the orbito-nasal vein. This vein in *Ethmopterus* has to go a considerable distance from the nasal sac to its foramen in the lamina orbitonosalis (figs. 95, 98, *o.n.v.*). During this passage it has become partly embedded in cartilage. Cartilage ridges arise dorsal and ventral to the vein. Rostrally these ridges embrace the vessel and enclose it in a canal. Anteriorly the vein is divided into two branches of which one (fig. 98) leaves the canal through a foramen, runs dorsal to the medial nasal cartilage, and enters the nasal capsule through the fenestra nasalis. The other branch enters the nasal capsule directly.[1]

[1] This description of the orbitonasal vein refers but to one specimen. There is, however, a great variability concerning this vein.

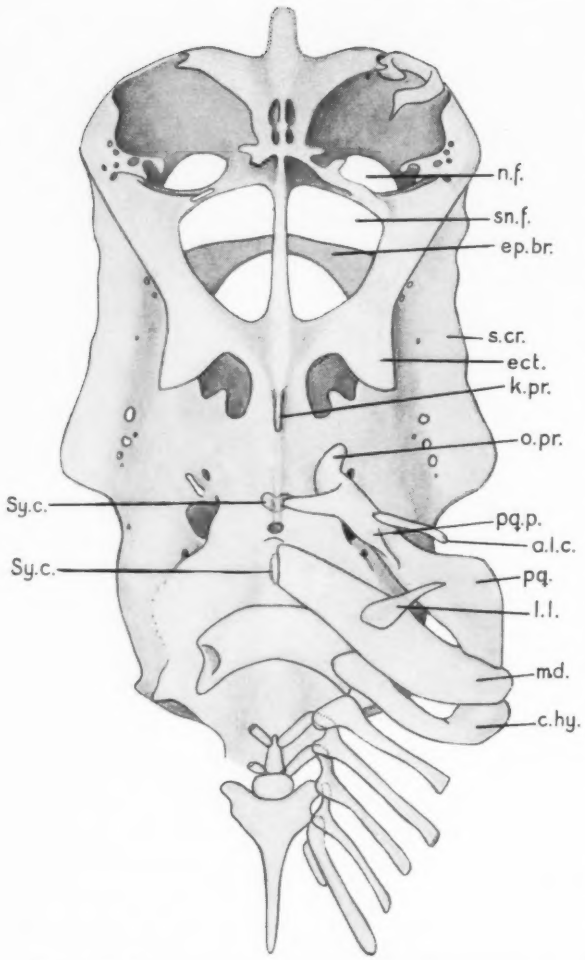

Fig. 96. *Etmopterus*. 55 mm. Skull. Reconstruction. Ventral aspect.

The medial area (keel) (fig. 96) is discernible from the praecarotid commissure caudally to the tip of the rostral process anteriorly. This latter process is chondrifying. Between the anterior tips of the palatine processes of the palatoquadrate, the medial area has given rise to the symphysial tissue which in this stage has a centre of chondrification on each side (fig. 96). K. FÜRBRINGER (1903) in a specimen of *Etmopterus spinax* has found four praespiracular cartilages. In the 55 mm embryo there are seven such cartilages present (fig. 95). Four of them undoubtedly correspond to those decribed by FÜRBRINGER. These lie external to each other. The most lateral is rudimentary, the second almost reaches the palatoquadrate. The remaining lie close to the three biggest of the cartilages and correspond probably to those branchlike thickenings, figured by FÜRBRINGER. These cartilages agree as to aspect and position with branchial rays. They are established independently as branchial rays and contemporaneously with the real rays, they develope from below and upwards from the mandibular arch. The praespiracular cartilages are evidently branchial rays of the mandibular arch and have a function of supporting the spiracular branchial lamellae. The palatoquadrate of *Etmopterus* anterior to the spiracular cartilages has a "processus oticus". This process, however, as described before, is derived in part from an independent rudiment, the extrapalatoquadrate and therefore scarcely could be any otic

process as that in Dipnoi and Amphibians.

The epithelial dental lamina extends to the posterior end of the palatine part of the palatoquadrate, and, as an epithelial thickening, a small distance on the palatoquadrate proper.

The lateral limbs of the V-shaped cartilage have separated from its medial portion and form the hypobranchials of the 2nd branchial arch (fig. 96). The medial portion represents the corresponding copula. A second copula is now present. It has been cut out from the anterior margin of the big posterior copular plate. This margin herewith has become concave, the anterior corners of it probably representing the hypobranchials 4. On the inside of the ceratobranchial of the fifth arch an oblong cartilage element

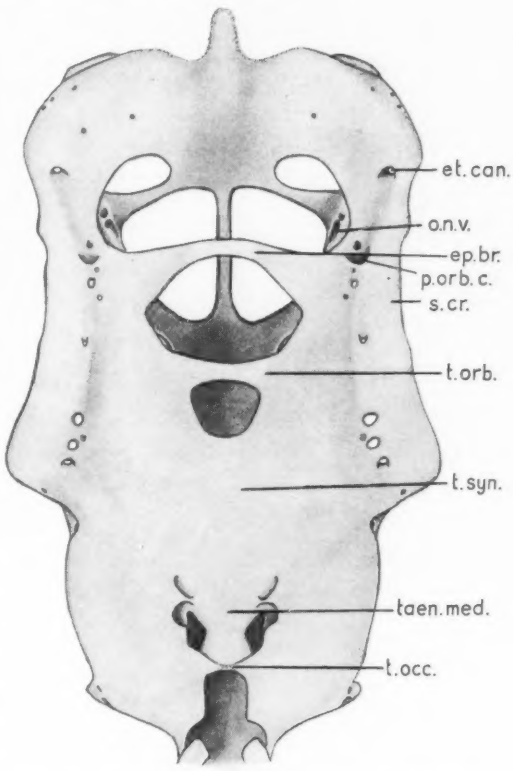

Fig. 97. *Etmopterus*. 55 mm. Skull. Reconstruction. Dorsal aspect.

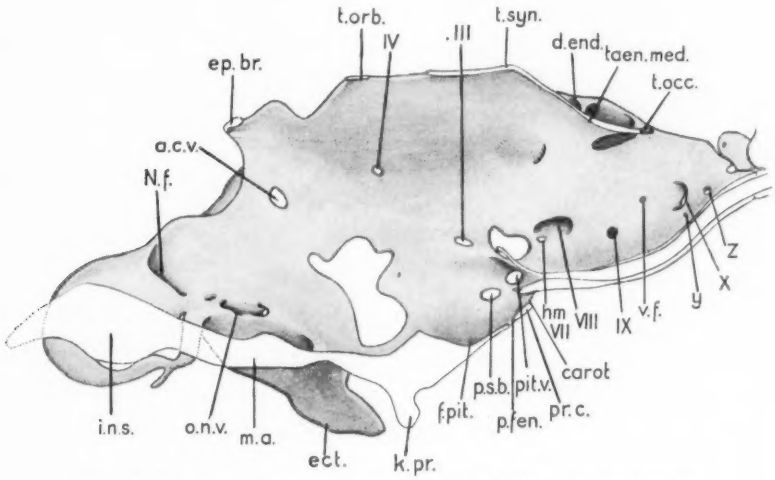

Fig. 98. *Etmopterus*. 55 mm. Skull, medial section. Reconstruction.

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is differentiated. A similar element has been figured by GEGENBAUR, but at the outside of the arch. He holds it to be a product of branchial arches. KÄLLBERG thinks that it corresponds to the caudad directed processes of the other ceratobranchials. The figure of the adult branchial basket given by GEGENBAUR suggests that a number of changes may take place after the 55 mm stage. None of these is, however, of fundamental importance, therefore the description of the development in *Etmopterus* may end with this stage.

SCYLLIUM CANICULA.

From GEGENBAUR's work on the Selachian skull (1872) it is evident that the sharks with some exceptions could be arranged in two great principal groups. A striking difference between these is found in the construction of the rostral structure. In one of these groups the rostrum is simple as in *Squalus*, in the other it is 3-rayed as in *Scyllium*. REGAN in 1906 divided the sharks with the exception of the *Notidanids*, into two great groups: the *Squaloidei*[1] and the *Galeoidei*. These groups not only differ with regard to the rostrum, but also with regard to many other characteristics. In the development of the skull the differences are especially very conspicuous. An embryological comparison was made by SEWERTZOFF (1899) while working out the development of the skull in *Squalus* and in *Pristiurus*. VAN WIJHE (1904, 1922) and GOODRICH (1918) worked out some points in the development of the skull of *Scyllium*, but since the classical work of PARKER (1875) a continuous investigation of this fish was not published until 1931, when DE BEER published a paper based upon a great number of embryonic stages. He used to a great extent van WIJHE's method of total stainings. This very instructive method has, however, the disadvantage that the blastemas, so very important for research, do not stain and are therefore lost. Also the prochondrium and the very young cartilage do not stain sufficiently. But since the method was controlled by serial sections, DE BEER's paper is of great value, especially with regard to the process of chondrification. The following investigation was made in order to fill in gaps in our knowledge and build up a firmer ground for comparisons.

Scyllium, stages from 2.5—18 mm.

These stages differ so very little from those younger stages of *Squalus* described in the preceding pages that it is not necessary to give any special description of them. The *Scyllium* stage of 18 mm corresponds rather well to the 16.5 mm stage of *Squalus*. It must, however, be pointed out that in

[1] *Rhina* and *Heterodontus* as well as the Cochliodonts and Hybodonts were refered to the *Squaloidei*.

Scyllium the ectomesoderm is less dense than in *Squalus*, and that therefore the mesenchymatic areas in younger stages are not so distinctly outlined as in *Squalus*. In more advanced stages, however, they are as distinct as in *Squalus*.

A comparison between the early embryos of *Scyllium* with those of *Squalus* and *Etmopterus* shows that the rudiment of the nasal organ in the latter generally lies much further forward than in *Scyllium*, where the brain flexure is much more pronounced than in the others. There, the distance between the nasal rudiments and the oral arch is much shorter than in the squaloids mentioned, and the angle between the parachordals and the trabecular rudiments considerably greater. This is a statement of some interest as it has been said that in *Scyllium* the trabecular angle should be considerably smaller than in other sharks. The shorter distance between the nasal sac and the oral arch has consequences regarding the development of the medial area as will be demonstrated further on.

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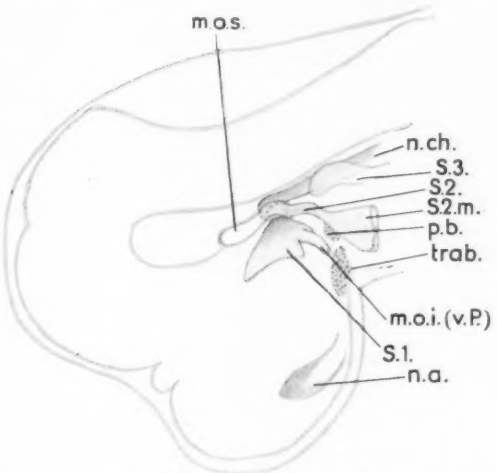

Fig. 99. *Scyllium*. 18 mm. Skull. Prootic part. Reconstruction. Lateral aspect.

Scyllium canicula, stage 18 mm.

In the 18 mm stage the polar cartilage and the trabeculae are very diffusely foreshadoed in the mesenchyma. The premandibular somite is well developed, with a large lumen. On its caudolateral part a long fingerlike evagination (fig. 99, *m.o.i. (v.P.)*) represents probably the vesicle of PLATT, as it gives origin to the inferior *obliquus* muscle of the eye.

Scyllium, stage 23.5 mm.

The notochordal hook as in all earlier stages is also present in the 23.5 mm stage and as a matter of fact is preserved until the 27 mm stage. The statement of GOODRICH (1918) and DE BEER (1931) that there should be no hook in *Scyllium*, thus is only valid for older stages above 27 mm body length.

In the 23.5 mm stage the mandibular as well as the hyoid head cavities have disappeared, but the premandibular cavity is always present as a big sac inside the eye. The premandibular commissure is also present but without a lumen. The postocular recess (vesicle of PLATT) of the cavity, well developed in the 18 mm stage, is now about to disappear but instead the obliquus inferior

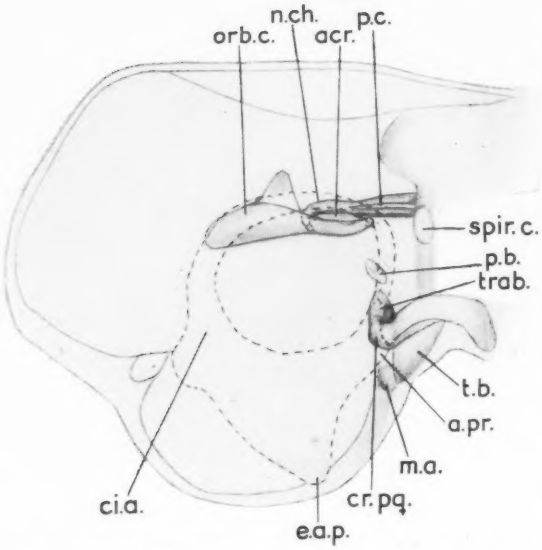

Fig. 100. *Scyllium*. 23.5 mm. Skull. Prootic part. Reconstruction. Lateral aspect.

muscle is developing. The preauditory part of the parachordal forms a pointed triangular lamella not reaching so far frontally as the premandibular commissure. The parachordal at the level of the anterior part of the auditory organ is much broader than in *Squalus* and *Etmopterus* and displays no signs of degeneration.

In the 23.5 mm stage the anterior and posterior rudiments of the auditory capsule already form a single blastematic lamella ventrolateral and lateral to the auditory vesicle, which is beginning to differentiate. The anterior and posterior basicapsular commissure blastemas are already connected with this lamella.

The polar cartilage (figs 100, 101, *p.b.*) is present as a heap of mesenchymatic cells immediately behind the medially directed part of the efferent pseudobranchial artery. The rudiment lies far below the level of the notochord and of the parachordals. Ventral to the rudiment of the polar cartilage and scarcely separated from it lies a diffuse condensation of the mesenchyma, representing the trabecula. Lateral to the lower end of the trabecular rudiments lies the anterior end of the more condensed rudiment of the mandibular arch. Towards this condensation the trabecula extends a diffusely outlined pro-

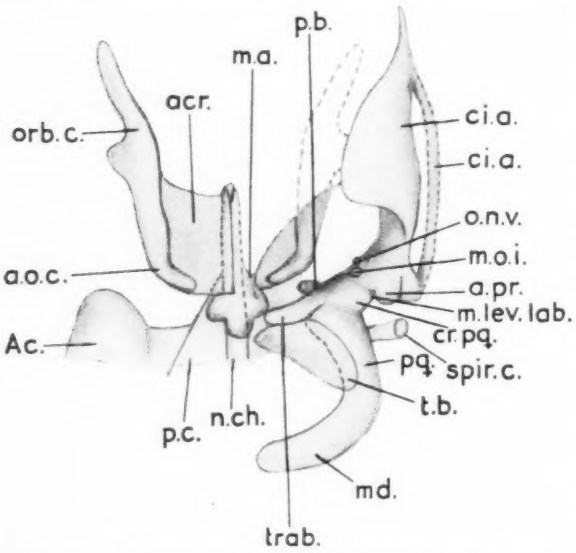

Fig. 101. *Scyllium*. 23.5 mm. Skull. Prootic part. Reconstruction. Ventral aspect.

cess (figs. 100—102, *cr.pq.*) on the dorsal side of which the obliquus inferior muscle of the eye is inserted. There is no distinct boundary between the trabecular process (cranio-palatoquadrate connection) and the palatoquadrate blastema, nor is there any distinct boundary between this process and the orbitonasal lamina which only caudally is separated from the eyebrow area. In this part of the orbitonasal lamina a blunt process (figs. 100, 101, *a.pr.*) represents the "antorbital process". The trabecular rudiment ventro-medially meets the deep portion of the medial area. The medial area (fig. 100, 101, *m.a.*) owing to the caudal situation of the nasal organs is rather short. It lies nearly perpendicularly to the lengthwise axis of the embryo. Its superficial part is broad and its deeper parts enter as a thick wedge between the anterior (lower) ends of the trabeculae and the posterior parts of the nasal sacs. Frontally the deep part of the medial area broadens strongly but simultanously becomes very indistinct.

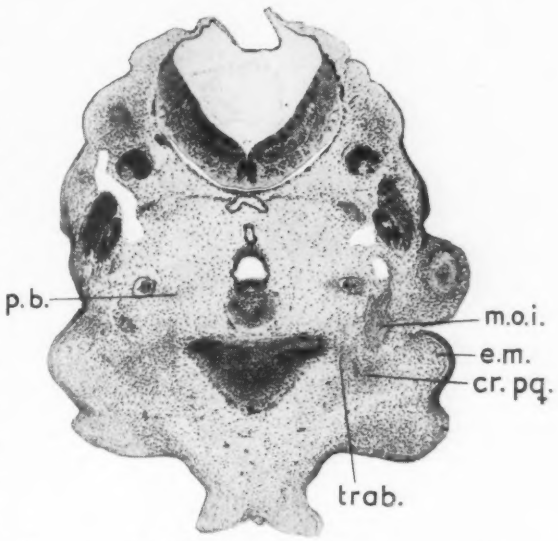

Fig. 102. *Scyllium*. 23.5 mm. Transverse section taken through the trabecular region.

The anterior end of the notochord rests upon the acrochordal tissue (figs. 100, 101, *acr.*) which extends posteriorly somewhat behind the anterior tip of the parachordals (*p.c.*). Embedded in, and confluent with this tissue are the posterior ends of the orbital cartilages (*orb.c.*). In the 23.5 mm stage these skeletal elements are quite blastematic. Anteriorly they merge into the supraorbital mesenchymatic area as in *Squalus*. Their other relations are as in *Squalus*.

The primary nasal capsule surrounds the nasal sac with a rather thick blastematic lamella which is condensed around the nasal opening there forming the rudiment of the annular cartilage.

The profundus nerve is present in the stages below the 23.5 mm stage but in this stage it is clearly seen that its anterior part is degenerating. In the 27.5 mm stage this part of the nerve has disappeared, and its posterior ciliar branch only could be found.

Scyllium, stage 27.5 mm.

The notochord has no end-hook from this stage on. In addition its anterior part is thicker than in *Squalus* and *Etmopterus*.

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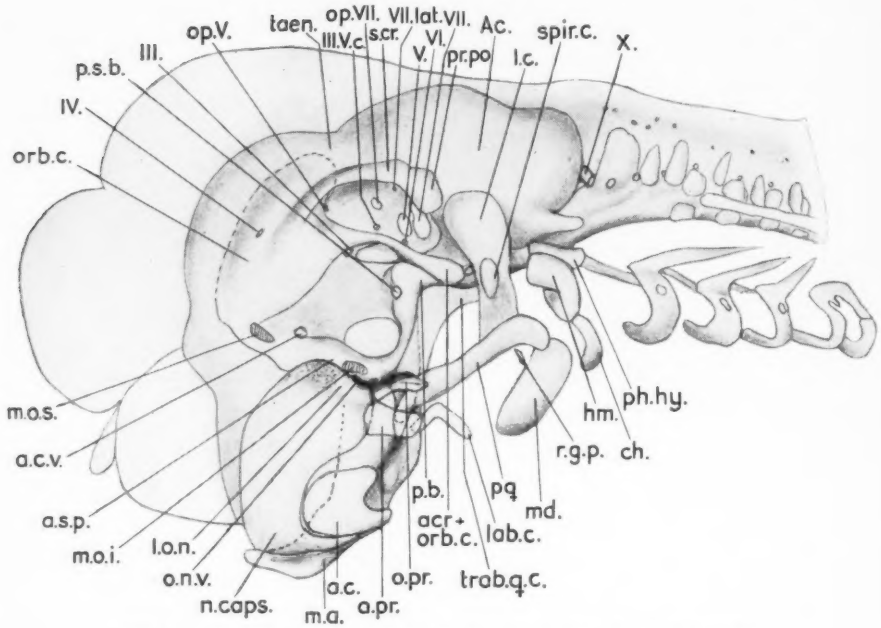

Fig. 103. *Scyllium*. 27.5 mm. Skull. Reconstruction. Lateral aspect.

Those parts of the parachordals, lying anterior to the auditory capsule, are not set against the most lateral parts of the notochord but against the dorsolateral. They are not, except in their foremost portion, as in *Squalus* and *Etmopterus* thickened towards the notochord but rather the contrary. In front the parachordals (fig. 104, *p.c.*) end with an acute angle as in *Squalus* and *Etmopterus*. The parachordals are considerably broader in the auditory region than in the Squaloids and the incisure between them and the anterior auditory cartilage is less deep. The lamina basiotica is broader. The rudiments of the auditory cartilages enclose the main part of the labyrinth organs. The blastema of the floor of the capsule, is somewhat more advanced than that of the rest of it. This more advanced blastema forms the basicapsular commissures and the mesotic plate (VAN WIJHE). Between the basicapsular commissures the fenestra basicapsularis (fig. 104, *f.bc.*) is enclosed. The posterior border of the posterior commissure (fig. 104, *p.bc.c.*) forms a kind of shelf below the glosopharyngeal nerve. The lateral border of the posterior commissure in front of the nerve is connected with the auditory capsule blastema, closing the glossopharyngeal foramen on the lateral side. The 27.5 mm stage from Roscoff, here under consideration, almost corresponds to the 29.5 mm or 30 mm stages of DE BEER from Naples. A comparison, however, is impossible, as DE BEER's description rests upon VAN WIJHE's stained preparations, where blastematic or young prochondrial parts are not well visible.

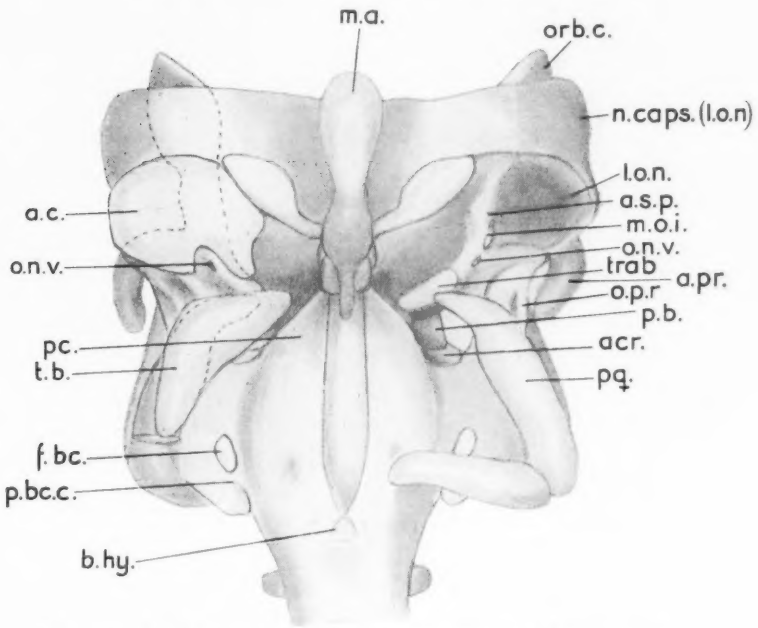

Fig. 104. *Scyllium*. 27.5 mm. Skull. Reconstruction. Ventral aspect.

The medial wall of the auditory capsule consits of the processus dorsalis, developed anterior to the glossopharyngeal nerve.

VAN WIJHE says (1922) that the cartilaginous elements of the vertebral column are formed as in *Squalus*, but DE BEER says that he has found no traces of basal bands, the basidorsals and basiventrals originating separately. KÄLLBERG's investigations confirm the findings of VAN WIHJE, but with the exception that the dorsal and ventral basal bands do not fuse until the different cartilages have developed (fig. 103). The basal bands are established as a prochondrium, which assumes the character of young cartilage in those parts situated nearest the notochord. From the dorsal basal band a blastema rises along the spinal cord. Dorsal to every basidorsal there issues a ventral spinal root. Anterior to these roots, and thus somewhat anterior to the basidorsals, the vertebral arches are formed (fig. 103). The two foremost originate independently.

The polar cartilages are placed (figs. 103—106, *p.b.*) on the lower side of the anterior part of the parachordals as DE BEER says. They are inserted more laterally than in *Squalus* and *Etmopterus* but in a manner corresponding to that in these genera, viz., by means of the acrochordal tissue to which the orbital (antotic) cartilages also (figs. 103—106, *acr.*, *acr* + *orb.c.*) are fused. The mode of insertion of these parts is not fully discernible in the 27.5 mm stage as fusions here have already taken place,

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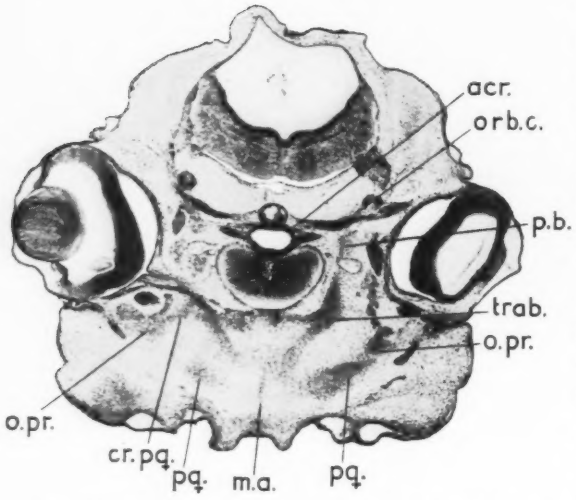

Fig. 105. *Scyllium*. 27.5 mm. Transverse section of the head region.

but in a 27 mm stage the relations are clearly distinguishable. There it is obvious 1. that the acrochordal tissue is present much as in *Etmopterus* and *Squalus* on the lower side of the notochord and that it has the wings described by VAN WIJHE in *Squalus*, 2. that the lateral and dorsal parts of the wings chondrify, 3. that the orbital cartilages join the lateral chondrified part of the wings and also although more caudally the lateral edge of the parachordals, 4. that the polar cartilages are inserted upon the basal antotic part of the orbital cartilage (fig. 107). Furthermore some part (frontal) of the insertion surface ought to belong to the acrochordal tissue proper.

The trabeculae are connected with the polar cartilages (fig. 103, *p.b.*). According to GOODRICH the former should originate in about the same plane as the parachordals. DE BEER's results (1931), with which mine agree rather well, oppose this view. Even if the angle between the trabeculae and the parachordals of my 27.5 mm stage does not attain 90°, it is considerable —about 73—75°. In front the trabeculae (fig. 104, *trab.*) bend somewhat laterad. In no part do they meet medially, the connection between the two trabeculae being established by the deep part of the medial area (fig. 105, *m.a.*), which forms the medial part of the trabecular plate. From the frontal part of each trabecula issues at nearly a right angle the "anterior sideplate", (figs. 103, 104, *a.s.p.*), which connects with the anterior end of the orbital cartilage. The sideplate forms the orbital wall, anterior to the optic fenestra and the orbital foramen of the anterior cerebral vein (fig. 103, *a.c.v.*), and posterior to the foramen of the orbitonasal vein (figs. 103, 104, *o.n.v.*). On its ventral part the obliquus inferior muscle (figs. 103, 104, *m.o.i.*) of the eye is inserted. At the anterior (lower) margin of the sideplate the posterior, thickened part of the orbitonasal lamina (nasal capsule) figs. 103, 104, *l.o.n.*) is fixed. This thickened part of the lamina is caudally continuous with a thick blastematic lamella, medially connected with the sideplate and witn the trabecula, caudally with the palatoquadrate (fig. 104, *o.pr.*). The posterolateral part of this lamella is about to chondrify forming through fusion with the palato-

quadrate its orbital process (figs. 103—105, *a. pr.*). This connection between the trabecula and the palatoquadrate represents the lateral process of the trabecula on which in earlier stages the m. obliquus inferior is inserted. At the posterior corner of the ventral border of the orbitonasal lamina the mesenchymatic rudiment of the "antorbital process" (figs. 103, 104, *o.pr.*) is inserted. In this stage it has partly delaminated from the lower eyebrow area. The mesenchymatic commissure between the palatoquadrate and the trabecula described in the preceding lines is part of a more extensive connection (figs. 103, 107, *trab.q.c.*, figs. 105, 106, *cr.pq.*) extending from the tip of the trabecula (and from the medial part of the trabecular plate) along the trabecula to the polar cartilage and from there caudad to the complex of the prespiracular cartilages. This connection is a rather thin lamella inserting on the anterior part of the palatoquadrate. The intermedial and superficial part of the medial area form the rather strongly developed blastema of the rostral keel and rod (*m.a.*). In the preceding stage this blastema is a short cellmass lying at the lower end of the trabecula. Owing to the straightening out of the cranial flexure the ventral outline of the head has lengthened and the nasal sacs have moved frontad. The consequence of this development is that the medial area is now longer. In this process the development of a nasal capsule rudiment has played some part. The medial area now extends as a rather broad perpendicular medial band of blastema from the hypophysial fenestra caudally between the palatoquadrates, and frontally

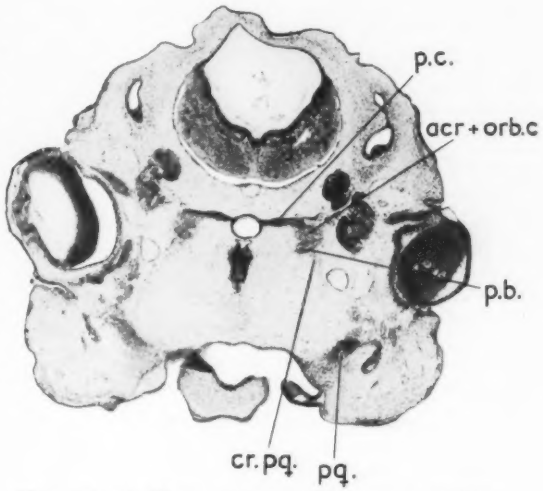

Fig. 106. *Scyllium*. 27.5 mm. Transverse section of the head region.

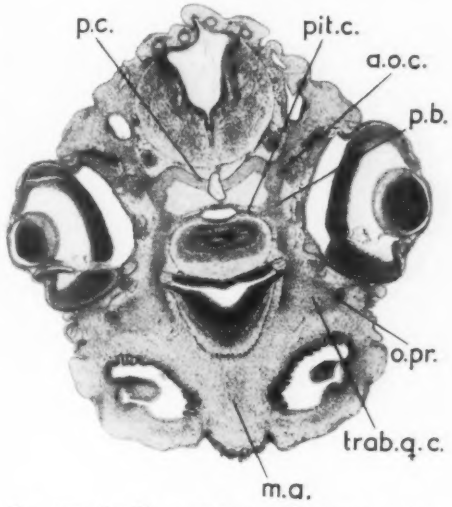

Fig. 107. *Scyllium*. 27.5 mm. Transverse section of the head region.

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past the nasal vesicles (figs. 103, 104, *m.a.*). The deep part of the medial area forms a lamellar ventral wall of the cranial cavity. It is laterally connected with the trabeculae and with the lower (posterior) part of the anterior sideplate. Seen from below the medial area has in its posterior part three broadened parts belonging to the superficial, the medium and the deep parts respectively (fig. 104).

The annular cartilage (*a.c.*) of the nasal capsule is as usual foreshadowed by a blastema. Anteriorly this blastema is continuous with a thin blastematic lamella which is medially connected with the anterior end of the medial area. Laterally this lamella embraces the forebrain to attain dorsally the anterior orbital frame. It forms the lateral wall of the secondary nasal capsule (figs. 103, 104, *n.caps.* or *l.o.n.*). Caudally it thickens into a ridge which forms the posterior border of the nasal capsule. This lamella is the orbitonasal lamella. It extends from in front, inside and below the nasal sac, and is also attached to the medial area. This part of the lamella constitutes the antero-mesial part of the nasal capsule. Its lateral and posterior part is thickened and forms a somewhat clubshaped body (fig. 104) between a superficial swelling of the medial area and the annular cartilage rudiment.

The orbital cartilage (fig. 103 *orb.c.*) is a broad cartilaginous lamella, pierced by the trochlear nerve (*IV.*). The pila antotica is rodlike and inserted on the acrochordal tissue as described above. From the orbital lamella a broad mesenchymatic bridge (fig. 103, *taen*) extends caudad toward the auditory capsule rudiment. Along the lateral border of this bridge runs the rudiment of the supraorbital crest (fig. 103, *s.cr.*), which, on the anterior part of the auditory capsule, widens to a postorbital process (fig. 103, *pr.po.*). The fissura prootica is covered by membrane which is pierced by the following nerves. In front lies the foramen of the ophthalmicus superficialis V nerve (fig. 103, *op.V.*). Some distance caudal to this lies dorsally the opthalmicus superficialis VII foramen (*op. VII.*) and below it the foramen of the oculomotorio-trigeminal commissure (*III.V.c.*). In the upper part of the fissures lies a small lateralis foramen (*VII.lat.*) and in the angle between the parachordale and the otic capsule, the trigeminal (*V.*), facialis (*VII.*) and abducens (*VI.*) foramina. All these foramina are separated by membrane, probably capable of chondrifying.

The palatoquadrate is about to chondrify; its mediad directed frontal end, the palatine process, however, is not even prochondrial and still not well differentiated from its dental blastema (fig. 104, *t.b.*). The connection between the palatoquadrate, the lamina orbitonasalis, the trabecula, etc., was described in the preceding pages. This connection,—the cranio-palatoquadrate —,was already present, in the 23.5 mm stage.

As in *Squalus* and *Etmopterus* the prespiracular complex is connected with the palatoquadrate. No muscular process blastema (extra-palatoquadrate) is present on the lateral side of the palatoquadrate.

The hyomandibula (fig. 103, *hm.*) of the 27.5 mm stage is very distinctly composed of three parts, viz, a dorsal, a medium and a ventral. The dorsal the pharyngohyal (*ph.hy.*), consists of a longitudinal blastema which is continued caudally by a ligament connecting with the epibranchial part of the first branchial arch. This blastema lies rather distant from the otic capsule rudiment. The medium part is the main part of the hyomandibula. It is prochondrial and corresponds to an epal element. The ventral part of the hyomandibula is blastematic. It is not quite free of the medium part in the 27.5 mm stage. On this part inserts the levator hyomandibular muscle (constrictor dorsalis). The morphological importance of these parts will be discussed later. The dorsal part of the hyomandibula later entirely fuses with the medium.

The branchial skeleton behaves as in *Squalus*. The "basihyal" (fig. 104, *b.hy.*) is unpaired.

Scyllium, stage 30 mm.

This stage does not differ much from the preceding (fig. 108). In the auditory capsule a rudiment of the cartilage of the posterior semicircular canal (cartilage of KÄLLBERG) has appeared. It will, however, be described in the 31 mm stage where it is more developed.

In the rudiment of the lateral cartilage of the nasal capsule there has appeared a somewhat thickened prochondrial band, which bends around the side of the forebrain. From the ventral border of this band the capsule rudiment continues to border the annular cartilage laterally and frontally, extending mediad to the medial area. The clubshaped rudiment of the antero-mesial wall of the nasal capsule (anterior wall of the capsule according to DE BEER) is more distinct than in the preceding stage. Posteriorly the lamina orbitonasalis (lateral capsular wall) is thickened as in the preceding stage. The rudiment of the "antorbital cartilage" is fused to the posteroventral end of the lamina orbitonasalis and of the anterior sideplate. The trabecula and the palatoquadrate are related to the orbitonasal plate as described in the preceding stage.

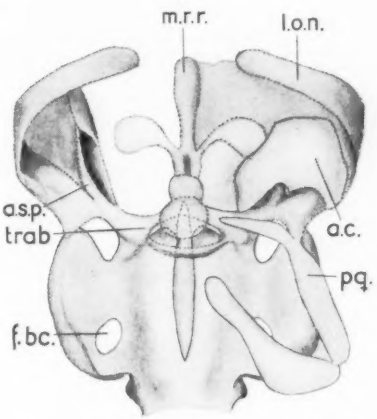

Fig. 108. *Scyllium*. 30 mm. Skull. Reconstruction. Ventral aspect.

Scyllium, stage 31 mm.

In the vertebral column the elements are chondrifying or have already chondrified. The auditory capsule is essentially established. To the rudiments already developed and described in the 27.5 mm stage is now added the rudiment of the cartilage of the posterior semicircular canal or the cartilage of KÄLLBERG (fig. 111, *c.K.*). Its development corresponds most closely to that in *Etmopterus* but differs in some details. As in *Etmopterus* it forms the medial lamellar wall of the auditory capsule posterior to the glossopharyngeal nerve. The lower border of this lamella bends laterad below the ventral side

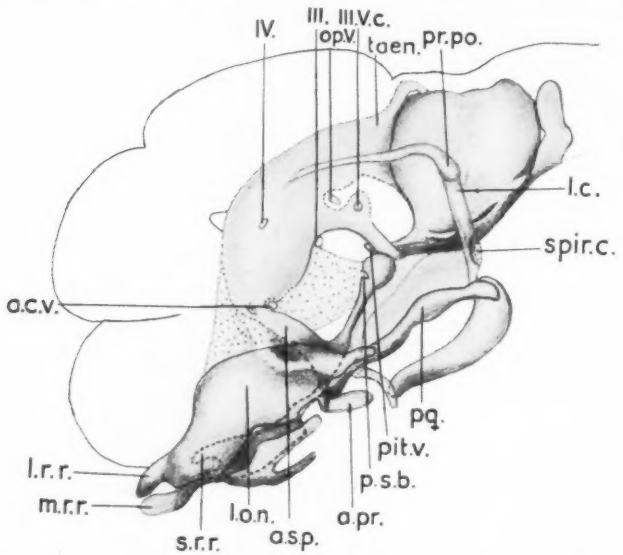

Fig. 109. *Scyllium*. 31 mm. Skull. Reconstruction. Lateral aspect.

of the lower part of the posterior semicircular canal without, however, reaching, its lateral side until further along caudally. From the vertical lamella, some distance behind the glossopharyngeal nerve and dorsal to the ventral limb of the posterior canal, there issues a prochondrial lamella (fig. 111, *c.K.l.*) which forms anteriorly a roof above the canal but bends down somewhat more caudally on its lateral side and finally fuses with the somewhat upbent lateral margin of the lower border of KÄLLBERG's cartilage. From the point where the two lamellas meet on the lateral side of the canal a cartilaginous rod (fig. 111 *c.K.r.*) belonging to the cartilage of KÄLLBERG extends frontad on the lateral side of the semicircular canal. This rod ends frontally immediately behind the glossopharyngeal nerve. Where the canal bends dorsad posteriorly, it is enclosed in the posterior part of KÄLLBERG's cartilage, which thus forms the caudal pole of the auditory capsule. In *Etmopterus* the posterior

part is broad, in *Scyllium* relatively narrow. Therefore the part taken in *Scyllium* by KÄLLBERG's cartilage in the formation of the posterior part of the auditory capsule is much less than that in *Etmopterus*. The glossopharyngeal nerve runs lateral to the cartilage of KÄLLBERG, enclosed by this cartilage (medially), the posterior auditory commissure (ventrally) and the auditory cartilage (dorsally and laterally).

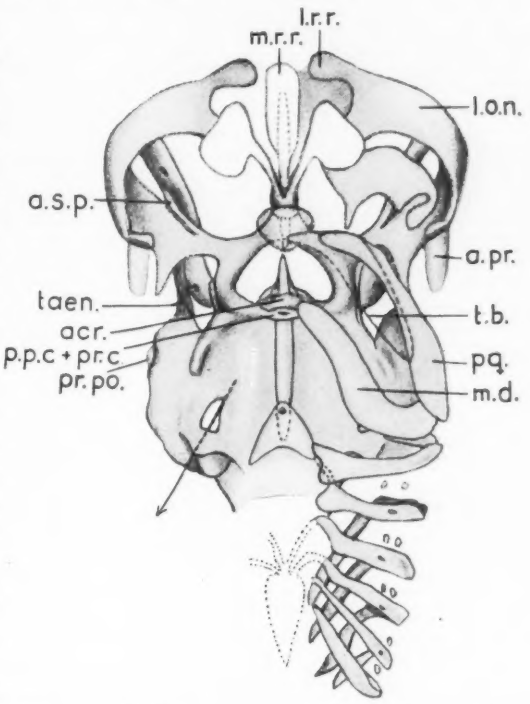

Fig. 110. *Scyllium*. 31 mm. Skull. Reconstruction. Ventral aspect.

The angle between the trabeculae and the parachordals almost has disappeared (fig. 109). The polar fig. 112, *p.b.*) and orbital cartilages have fused with the chondrified part of the acrochordal tissue (*acr.*) and by means of this tissue with the parachordals (*p.c.*). In front there is left a fissure between the polar and the antotic cartilage, and between the latter and the acrochordal tissue and the parachordals. Caudally all these structures are fused, the fused acrochordal tissue and the antotic cartilage being discernible as caudad diverging thickenings at the lateral border of the parachordals. These thickenings run out caudally toward the rudiments of the subotical shelf. (See below!). The frontal part of the acrochordal tissue forms a wing on each side of the notochord. The wings are connected with each other below the notochord in their posterior part. Postpituitary (fig. 110, *p.p.c.*) as well as precarotic commissures (fig. 110, 112, *pr.c.*) are present between the polar cartilages. They issue on each side from a common

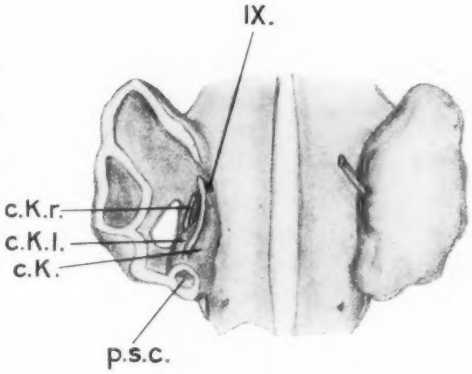

Fig. 111. *Scyllium*. 31 mm. Otic region. Reconstruction. Dorsal aspect. The left auditory capsule opened.

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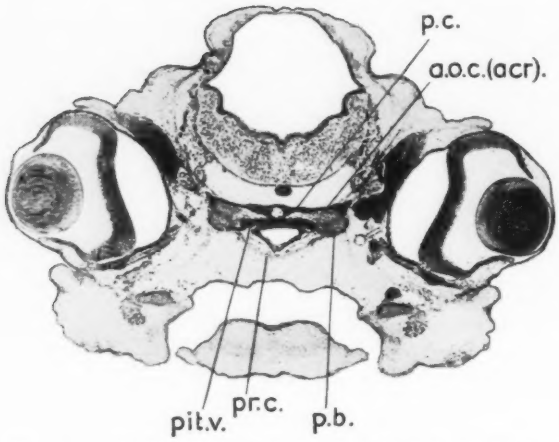

Fig. 112. *Scyllium*. 31 mm. Section through the acrochordal region of the head.

stem continuous with the polar cartilage. DE BEER has figured a wide fenestra behind them. I have not found such a fenestra. The postpituitary commissure in *Scyllium* is not as in *Squalus* fused with the acrochordal tissue below the parachordals, but is a separate commissure as slender as the precarotid and separated by a fissure from the acrochordal tissue. The orbital cartilage is connected by means of a taenia marginalis (figs. 109, 110, *taen.*) with the anterior end of the auditory capsule, a relatively independent dorsal limb connecting with the medial anterodorsal part of the capsule.

The supraorbital crest (fig. 109) is about to form from the upper eyebrow area. In the 27.5 mm stage this crest is quite mesenchymatic. It is formed by the mesenchyma of this area and has a very slight connection with the orbital cartilage. In the 31 mm stage a medial part of this mesenchyma is about to chondrify as a low but sharp ridge on the outside of the posterior half of the cartilage. This ridge continues on the taenia marginalis to the outside of the auditory capsule where it forms a rather broad postorbital process (figs. 109, 110, *pr.po.*).

A prochondrial lamella connected with the pila antotica separates (imperfectly) the nervus ophthalmicus superficialis V (fig. 109, *op.V.*) from the ophthalmicus superficialis VII and the trigemino-facialis nerves. In the lamella the commissure (*III., V.c.*) between the trigeminal and the oculomotor nerves is enclosed in a small foramen. The foramina of the efferent pseudobranchial (fig. 109, *p.s.b.*) artery and the pituitary vein (figs. 109, 112, *pit.v.*) develop as in *Squalus* and *Etmopterus*.

In the anterior parts of the skull this embryo differs from all stages described by DE BEER, probably because in his figures the blastemas and prochondrial tissues have not been represented. The anterior sideplates (figs. 109, 110, *a.s.p.*) reach the orbital cartilage. The existence of a notch for the anterior cerebral vein (fig. 109, *a.c.v.*) in the orbital cartilage behind the point where the sideplate reaches it gives evidence for the correspondence of this sideplate with that in *Squalus*. The lamina orbitonasalis is connected with it for only a short distance. The lamina orbitonasalis (*l.o.n.*) forms the lateral

and frontal wall of the nasal capsule. Frontally it has a short process, which is the rudiment of one of the lateral rostral rods (figs. 109, 110, *l.r.r.*) of the adult *Scyllium*. The anterolateral wall of the nasal capsule has fused with its anteromesial rudiment (the clubshaped rudiment of earlier stages) (fig. 110). The posterior part of the lamina orbitonasalis is thickened as in the preceding stages (27.5, 30 mm), the thickening forming a low ridge on the outside of the nasal capsule (fig. 109). At the posteroventral margin of the nasal capsule a rather indistinct rudiment of the "antorbital process" (figs. 109, 110, *a.pr.*) is inserted. The thickened part of the lamina orbitonasalis seems to run out in a process connecting with the palatoquadrate (fig. 109, *pq.*).This process as described in the 27.5 mm stage does not, however, belong to the lamina orbitonasalis but rather corresponds to the primary lateral process of the trabecula on which the inferior obliquus muscle of the eye is inserted. In the 31 mm stage the lateral (posterior) part of this process is connected with the palatoquadrate and is chondrifying, whereas the medial part is about to transform into a ligamentous band. This band continues caudally along the trabecula to the prespiracular complex where it joins this structure including the rudiment of the otical shelf cartilage. The lower (lateral) border of this band becomes thinner than the upper by degrees and continues ventrally in a mesenchymatic lamella frontally distinct, caudally rather indistinct, which joins the palatoquadrate along its upper and inner margin. Thus the palatoquadrate is connected with the basis cranii throughout its length. The upper (medial) part of the lamella is the rudiment of the "subocular cartilage" or subocular shelf.

The medial area between the nasal capsules forms a high but thin internasal septum. The lower border (superficial part of the medial area) of the septum forms frontally the rostrum (medial rod of the rostrum of the adult). The upper border (deep part of the medial area) is also prolonged frontad below the forebrain, forming the "suprarostral" process (DE BEER) (fig. 109, *s.r.r.*).

The palatoquadrate is about to chondrify. Its anterior inbent end, however, is still blastematic and not yet fully divided into a superficial tooth blastema and a deeper palatine process. The anterior end of the palatoquadrate bends mediad, and the palatoquadrates (tooth-blastema) of the two sides are separated only by a vertical lamella belonging to the medial area which thus forms a primary symphysial tissue lamella. The mesenchymatic rudiment of the prespiracular complex (fig. 109, *spir.c.*) is connected with the posterior end of the palatoquadrate. This rudiment consists of an inner mesenchymatic band which rises to the postorbital process connecting on its way up with the basis cranii and thus forming between the ventrolateral border of the otic capsule and the postorbital process a canal enclosing the hyomandibular nerve and the jugular vein. In this way a mesenchymatic lateral commissure

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is formed. Connected with the outside of the prespiracular lamella and in front of the spiracle is situated an indistinctly outlined dense blastema, the rudiment of the prespiracular cartilage. No rudiment of any muscular process was found on the lateral side of the palatoquadrate.

The hyomandibula is as in the preceding stage. Its three parts are well differentiated from each other.

Scyllium, stage 38 mm.

In the occipital region a real perichordal commissure is present. Anterior to it the chondrified external notochordal sheath is uncovered by the parachordal cartilage. In the region of the polar cartilages the postpituitary commissure has joined the acrochordal tissue commissure, later to fuse with it and form an anterior slender cartilage bridge below the notochord. Dorsally the notochord is quite uncovered. These conditions, different from those in the *Squaloids*, are present also in a 90 mm embryo, where the considerably reduced notochord with its chondrified sheath separates the parachordals from each other excepting at two points, viz., in the occipital region, as stated above, and at the dorsum sellae, where the notochord rests upon cartilage. The dorsum sellae in KÄLLBERG's embryos differs from the descriptions of DE BEER. According to DE BEER two processes facing each other from the anterior diverging parts[1] of the parachordals are formed in the same region as the commissures enclosing the carotid artery, (dorsal to the commissures), These are said to be the rudiments of the dorsum sellae and behind them there is an opening, representing a fenestra basicranialis. Comparing DE BEER's figures one finds, that this fenestra is very variable, with an extension by no means corresponding to the age of the embryos. This probably depends on individual variations, but there is also the possibility that the fenestra really is closed by cartilage, as in his figure 11, but that the staining of the entire embryo has not succeeded well. All our specimens support this assumption. From the pila antotica, fused to the polar cartilages in the 38 mm stage, two mediad directed processes have arisen, corresponding to DE BEER's dorsum sellae rudiments. These, however, never reach each other in the midline but medially abut against, and fuse with, the acrochordal tissue + the parachordals. By this process an empty "foramen" (fig. 113, *c.f.*) arises on each side between the parachordal, the dorsum sellae and the polar cartilages. It is closed by membrane and soon also with cartilage. It represents the single remainder of the "fenestra basicranialis" that we could find in our embryos. The commissura postpituitaria lies close to the parachordal behind the pituitary vein. Later fusion takes place and the cartilage extends frontad, forming that medial part of the dorsum sellae lying below the notochord. The conditions in this region, owing to the slower development of the acrochordal

[1] The parachordals are said to diverge frontally.

tissue, differ considerably from that of the *Squaloids*. The fenestra hypophyseos is closed by chondrifying membrane (deep part of the medial area) and by the caudal growth of the trabecular plate (chondrifying medial area) and the frontal extension of the commissura praecarotidea. In the *Squaloids* the fenestra closes only from the front, but in *Scyllium* from behind as well.

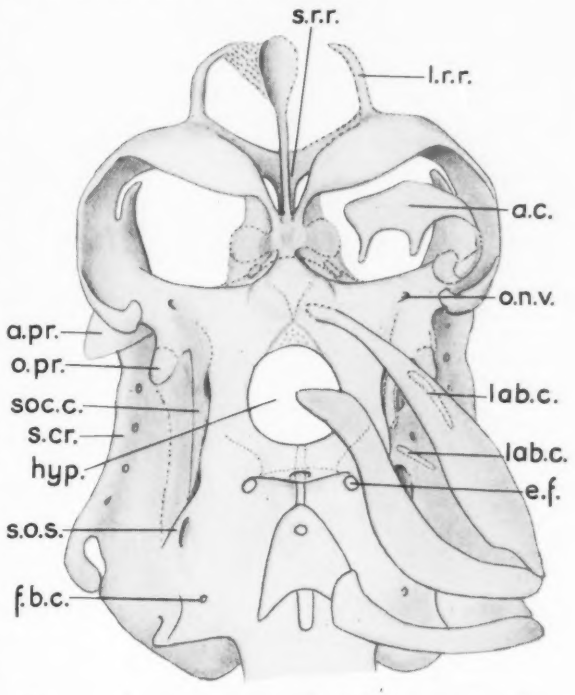

Fig. 113. *Scyllium*. 38 mm. Skull Reconstruction. Ventral aspect.

The auditory capsule is now a continuous cartilage. It is completely roofed. The occipital column, pierced by two occipital nerves, has united with the capsule dorsal to the vagus nerve. The glossopharyngeal canal has arisen as in *Etmopterus*. In the floor of the capsule there is a little foramen, designed by DE BEER as the point, where the "lamina hypotica" does not attain the real floor of the capsule. According to KÄLLBERG it is the remainder of the fenestra basicapsularis (fig. 113, *f.bc.*). The tectum synoticum is complete between the otic capsules. A tectum posterius (occipitalis) is also present. The latter develops earlier than the former.

In *Scyllium* the division of the foramen prooticum effected by chondrification of the membrane covering it in earlier stages results in a separation by cartilage of the nerves passing through the prootic fenestra. Through the upper foramina run the ramus ophthalmicus superficialis V and VII, already separated from each other by a secondary cartilage bridge. The lower part of the primary "prootic foramen" transmits the rest of the trigeminofacialis system and the abducens nerve. In *Squalus* and *Etmopterus* the upper part of the "foramen prooticum" is empty and closes.

The anterior sideplate (fig. 114, *a.s.p.*) is united with the orbital cartilage. Rostral to it the lamina orbitonasalis and the orbital cartilage have also fused. A preorbital cartilage (fig. 114, *pr.c.*) rudiment is present as a connecting link between the latter cartilages, lateral to the ophthalmicus nerve.

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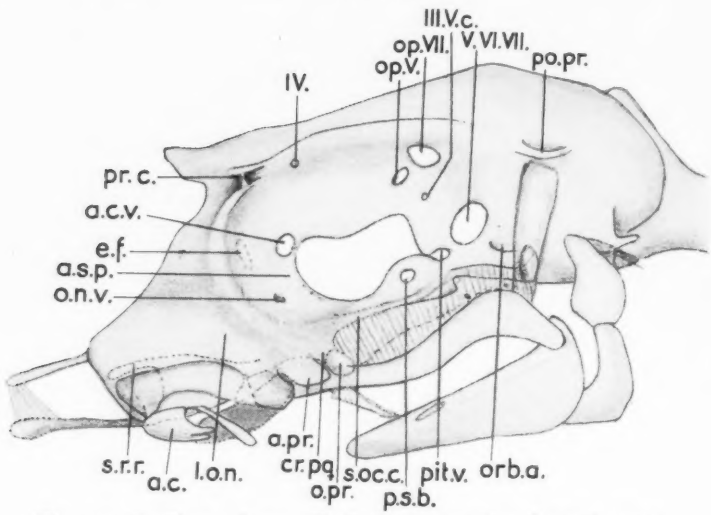

Fig. 114. *Scyllium*. 38 mm. Skull. Reconstruction. Lateral aspect.

This preorbital cartilage develops in the eyebrow area. The foramen of the orbitonasal vein (*o.n.v.*) and dorsal to it an empty foramen (fig. 114, *e.f.*) represent the remainders of the fissure between the anterior sideplate and the orbitonasal lamina. The empty foramen, later closing, probably corresponds to the foramen of the profundus nerve in *Squalus*. In *Scyllium* this nerve is lacking. DE BEER (1937) after comparing with *Heterodontus Philippi* says that the foramen of the orbitonasal vein should answer to the foramen through which a profundus nerve, if present, would leave the orbit. The orbitonasal foramen is present in *Squalus* and *Etmopterus* as well as in *Heterodontus japonicus*, all of them having the profundus nerve enclosed in a special foramen or in the foramen of the anterior cerebral vein (*Heterodontus*). In *Squalus* and *Etmopterus* the profundus foramen is enclosed in the orbitonasal plate anterior to the anterior side plate of the trabecula.

On the lateral side of the orbital cartilage lies the supraorbital crest (figs. 113, *s.cr.*). This ends caudally on the lateral surface of the auditory capsule. The supraorbital crest runs out posteriorly in a postorbital process which is not massive and conical as in *Squalus* but formed as a rod bending lateral to the sensory line canal in this region. Later the posterior end of the rod fuses with the auditory capsule and the sensory canal is thus overbridged by this structure. This postorbital process is secondary. It has developed from the eyebrow area in front of and outside the sensory canal and has joined secondarily the primary process present in earlier stages. The frontal part of the preorbital ridge is dorsally bent somewhat caudad, ventral to the supraorbital crest. Thus a groove arises between the two ridges. The united rami ophthalmici superficiales V. and VII. run in this groove. The preorbital

canal is formed by that not yet chondrified bridge lateral to the nerves (mentioned in the preceding lines). This bridge like that in Squaloids, probably has an independent origin. The ethmoidal canal is lacking owing to the facts that the frontal process of the eyebrow area does not join the nasal capsule, nor chondrify. The nerve passing the ethmoid canal in *Squalus*, thus runs on the outside of the skull in *Scyllium*.

The (subotical) shelf (figs. 113, *s.o.s.*), present in the 31 mm stage as a process behind the foramen prooticum, has now joined the otic capsule with its posterior tip. Anterior to this connection runs the orbital artery (DE BEER), which thus pirces the subotical shelf.

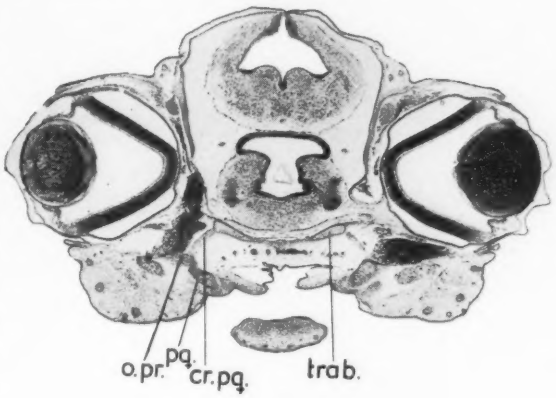

Fig. 115.

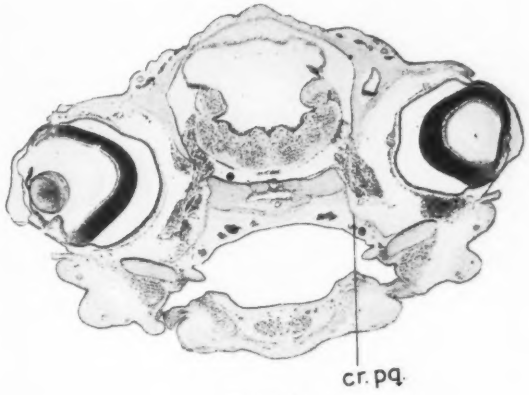

Fig. 116.

Figs. 115—116. *Scyllium*. 38 mm. Transverse section of the head region.

The anterior part of the subocular shelf (subocular cartilage) (figs. 113, 114, *s.oc.c.*) [SEWERTZOFF (1899), DE BEER (1931)] extends from the lamina orbitonasalis frontally to the subotical shelf caudally. Its most anterior part is continuous with that ligamentous band which connects the trabecula with the palatoquadrate. In the squaloid sharks from the caudal corners of the lamina orbitonasalis there extends a triangular lamella corresponding probably to the antorbital cartilage ("Flossenträgerknorpel") of the rays. A similar but smaller lamella (figs. 113, 114, *a.pr.*) also is present in *Scyllium*, inserted anterior to the cranio-quadrate connection (figs. 114, 115, *cr.pq.*). It is present in earlier stages, but in the 38 mm stage it becomes well outlined. As in preceding stages the palatoquadrate, now chondrified, is connected by a lamella partly with the posterior corner af the "lamina orbitonasalis" and partly with the trabecula (fig. 116, *cr.pq.*). This corner seems to be the

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thickened foremost part of the connecting lamella (fig. 114). It will later fuse with the palatoquadrate, and chondrifying, constitute the orbital process (*o.pr.*) of the palatoquadrate with its ligament. Thus the conditions in this embryo seem to indicate that the palatoquadrate, the cranioquadrate connection and the subocular cartilage form a complex, fused to or connected with the trabecula. These conditions will be discussed later.

The so-called suprarostral process (fig. 114, *s.r.r.*) continues frontally between the nasal sacs. It bifurcates anterior to them (fig. 113, *s.r.r.*), and dorsal to the antero-mesial nasal cartilage. Its lateral border is connected with the lateral nasal cartilage. It forms the dorsal wall of the most anterior part of the nasal capsule and simultanously the ventral wall of the cranial cavity in this region. The branches of the suprarostral rod thus also form the anterior boundary of the fenestra nasalis. This boundary cartilage GEGENBAUR (1892), SEWERTZOFF (1899) and MORI (1924) homologised with that bridge, dividing secondarily the nasal fenestra in *Squalus*. The subnasal fenestra of GEGENBAUR is thus considered to correspond to the space between the lateral and ventral rostral rods in *Scyllium*, and the nasal fenestra to represent the secondary nasal fenestra in *Squalus*. In *Etmopterus* the cartilage bridge separating the nasal and subnasal fenestrae runs transversely caudomedial to the olfactory tract. The subnasal fenestra thus lies behind the nasal fenestra. The anterior border of the "nasal fenestra" in *Scyllium* lies anterior and dorsal to the olfactory tract, and consequently ought to correspond to the posterior margin of the rostral plate in *Squalus*. Accordingly the "nasal fenestra" in *Scyllium* contains the true nasal fenestra together with the subnasal fenestra, and the two are not separated. The anterior mesial capsular wall (clubshaped lamella) (fig. 113) has fused with the anterior part of the lateral capsular wall forming the anteromesial wall of the nasal capsule. From this point of fusion there issue from the lateral cartilage the lateral rostral processes which, according to MORI, correspond to the nasal ridges in *Squalus*. The space between the rods should thus correspond to the space between the nasal ridges and the medial keel of the rostrum in *Squalus*. This interpretation seems at first to be well founded. The ontogeny of the rostrum in *Squalus*, however, suggest another. In *Squalus* the rostrum consists of the rostral keel, formed by the rostral and the suprarostral, and of a spoonlike section, the lateral extension of the suprarostral part (deep part of the medial area). In *Scyllium* the medial rostral rod is the superficial part of the rostral almost corresponding to the keel of the rostrum in *Squalus*. The lateral rostral rods in *Scyllium* have no corresponding parts in *Squalus* as they arise in connection with the lateral capsular wall and not with lateral expansions of the suprarostral (deep part of the medial area). In *Scyllium* such expansions are present but they there form the floor upon which the forebrain rests, a precerebral fossa like that in *Squalus* being absent.

There is in my material no other vein foramen behind the nasal fenestra beside the foramen orbito-nasale. (DE BEER figures another big foramen.)

The anteromesial capsular wall is continued caudally by a membranous medial wall of the nasal capsule. The posteroventral border of this membrane contains a blastematic thickening, which later grows larger and chondrifies, helping the nasal cartilage support the nasal flap. The nasal cartilage ("annular cartilage") is now transversely enlongated. It sends out two processes posteriorly. Its lateral corner is connected by a blastema with a new element (outer process of nasal cartilage) lying posterolateral to the nasal opening. This opening is surrounded by cartilage like a horseshoe. A complete annular enclosure of the aperture like that described by DE BEER in his 30 mm specimen has not been found in any of our stages.

The spiracular cartilage of this stage was found to contain two condensations. In another specimen labeled as 33 mm long, but apparently somewhat more developed than the 38 mm specimen, two distinct condensations were clearly seen. These condensations represent two rudiments of spiracular cartilages, viz. two mandibular branchial rays. These rudiments in the following stage fuse, forming the single spiracular cartilage present in *Scyllium*. As in the Squaloids the membranous rudiment of the lateral commissure is connected with the spiracular cartilages and with the posterior part of the palatoquadrate.

Two labial cartilages only are present, one upper and one lower. The upper cartilage corresponds to the anterior upper in *Squalus* and to the single (anterior) upper in *Etmopterus*.

Scyllium, stage 40 mm.

The fenestra hypophyseos is closed by young cartilage, thinner than that of the rest of the cranial floor. There is no foramen left for the hypophysial stalk (fig. 117).

The medial and the lateral rostral processes or rods are united anteriorly by a blastema forming the typical three-rayed rostrum of the Galeoids (figs 117, 118). The lateral rods of the rostrum now seem to issue from the anterior border of the "rostral plate" (deep part of the medial area, "suprarostral") but in a 90 mm stage they issue from the dorsal wall of the nasal capsule. In the preceding lines it has, however, been shown that they are formed from the lateral nasal cartilage ventral to the "rostral plate". They thus belong to the lamina orbitonasalis. The nasal capsule has been completed laterally by a dorsally chondrifying membrane connecting the ventral border of the orbitonasal lamina with the annular cartilage (fig. 118). In the reconstruction (fig. 117) the membrane is omitted. The posterior wall of the capsule is chondrified and thickened. A strong membranous inner wall containing, a rather small but thick cartilaginous nucleus has appeared (figs. 117, 118). On the dorsocaudal part of the posterior wall of the nasal capsule is

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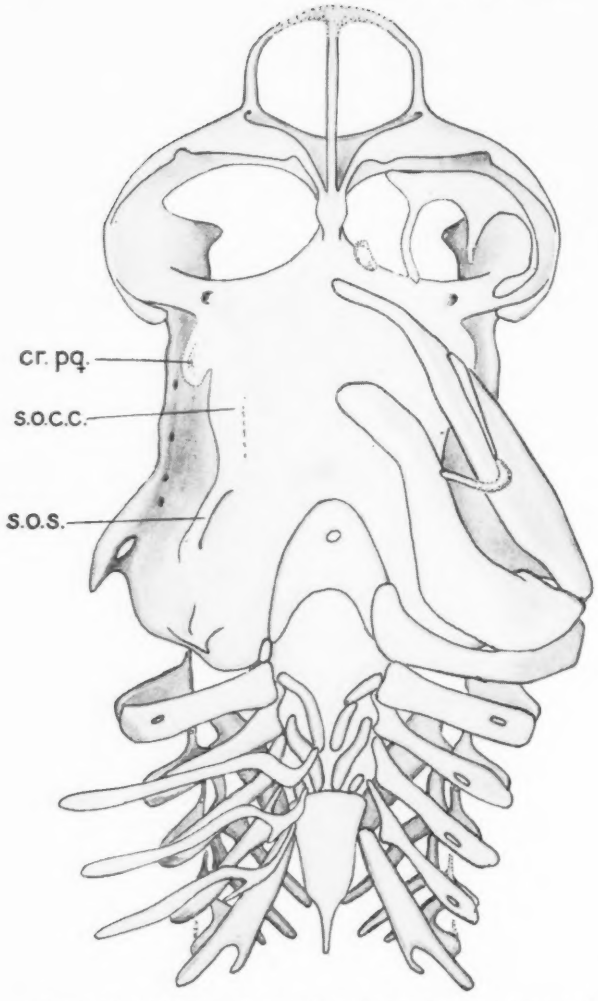

Fig. 117. *Scyllium*. 40 mm. Skull, membranous parts and lateral commissure omitted. Reconstruction. Ventral aspect.

inserted the membranous antorbital process (fig. 118, *a.pr.*), well separated from the cranio-quadrate connecting bridge. This antorbital process is pierced by a strong branch of the sensory buccalis VII. nerve.

The medial area, of which the superficial part forms rostrally the medial rostral rod, constitutes caudally the internasal septum. A posterior part has been detached from it forming a rather big blastema continuous with the tissue of the palatoquadrate symphysis. The deep part of the medial area (supra-rostral process) has broadened rostrally to a part of the floor of the cranial cavity in the most anterior part of the skull, at the same time forming the roof of the nasal capsule anterior to the nasal fenestra. That young cartilage closing up the hypophysial fenestra is probably formed by the deep part of the medial area, of which the other parts have disappeared.

The subocular shelf (figs. 117, 118, *s.o.c.s.*) and its connections will be described in this stage. The shelf extends as in the preceding stage along the trabecula, beginning in front with the cranio-quadrate connection, from which its anterior part can not be delimited. Its frontal part is connected with the palatoquadrate forming at the outside of it a prochondrial cushion, the rudiment of the orbital process (fig. 118, *o.pr.*). The connection of this cushion with the shelf proper is ligamentous and seems never fully to chondrify.

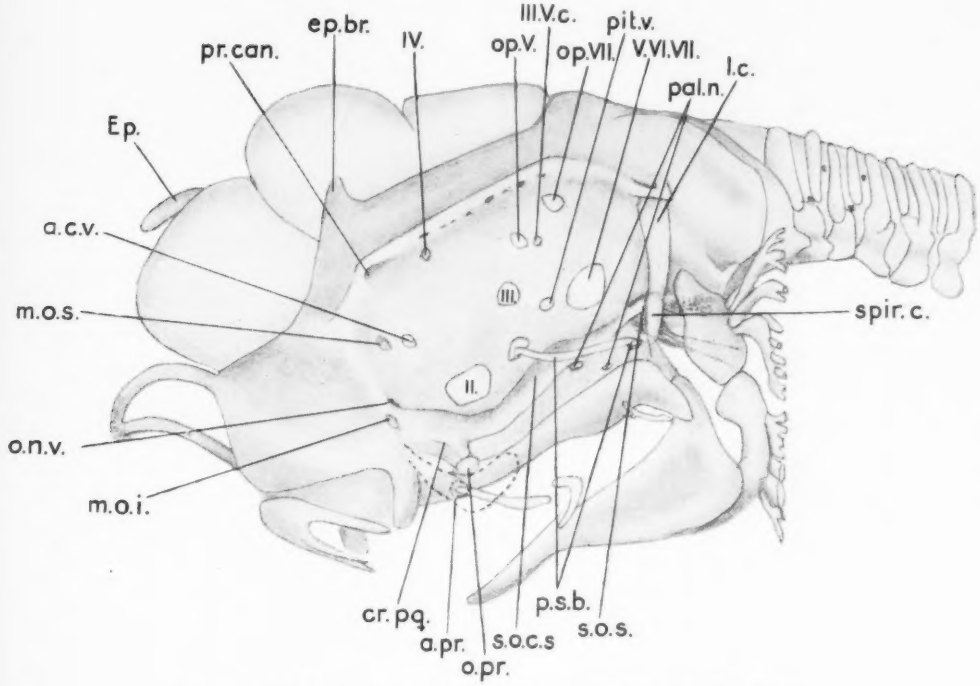

Fig. 118. *Scyllium*. 40 mm. Skull. Reconstruction. Lateral aspect.

Behind this anterior part the shelf consists of a broad lamella, thinning out laterally by degrees. This lamella is chondrifying along the trabecula, the chondrification decreasing laterad so that the most lateral thinnest part of the lamella is merely a thin membrane of connective tissue. There is no reason why we should not consider this thinnest part as belonging to the shelf, as well as its thicker parts. This lateral thin part is connected with the palatoquadrate along its inside. This connection extends from the cranio-quadrate connection (orbital process) to the posterior end of the palatoquadrate. Behind the prootic foramen, where the orbital artery ascends to the orbita, the chondrification of the shelf (figs. 117, 118, *s.o.s.*) (otical shelf of the preceding stage) is further advanced so that the artery is laterally bridged over by a completely chondrified shelf portion outside of which the shelf is less chondrified and extends as a prochondrial and laterally even membranous portion towards the palatoquadrate on which it is inserted, as already mentioned. Posterior to the orbital artery the shelf tissue alters, its lateral membranous part thickening and becoming ligamentous. At this thickened part are inserted first the lower end of the membranous lateral commissure (fig. 118, *l.c.*) of the neurocranium, and second the spiracular cartilages (fig. 118, *spir.c.*). The posterior end of the ligamentous, thickened shelf membrane forms

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posteriorly a strong ligament that inserts at the posterior end of the palatoquadrate above the mandibular articulation. That part of the shelf lying immediately outside of the cartilage bridge lateral to the orbital artery in the 40 mm stage is connected by a strong ligament with the inside of the lower part of the hyomandibula (fig. 118). These different conditions, very distinct in the 40 mm stage, could be traced back to the 30 mm stage, but in these earlier stages the different posterior elements form a single mesenchymatic plate indistinctly outlined and impossible to reconstruct in an instructive way.

The shelf as described above has the following relations to nerves and bloodvessels. Inside the (membraneous) lateral commissure pass the jugular vein and the hyomandibular nerve. The orbital artery passes inside the otical shelf cartilage. The efferent pseudobranchial artery, together with a posterior branch of the palatine nerve, passes through the membranous part of the subocular shelf a short distance in front of the spiracular cartilage. The artery thus pierces the shelf (fig. 118, *p.s.b.*) from below then proceeds dorsal to it to the pseudobranchial foramen in the ventral part of the orbita. Anterior to the last named shelf foramen there are two more foramina in the membranous part of the shelf, viz., the palatin foramen (fig. 118, *pal.n.*) in front and posterior to it a foramen for a branch of the palatin nerve. The consequences of the preceding description of the subocular shelf and its relations to the palatoquadrate will be treated in another part of this paper. The nerve and bloodvessel foramina of the neural cranium (fig. 118) are as in the adult skull. There is no chondrified prefacial commissure. The trigeminal and the hyomandibularis VII. nerves both run through the prootic foramen separated, of course, by membrane. The abducens nerve also passes through it. The eyestalk is missing.

In the auditory capsule the cartilage bridge encircling the anterior semicircular canal between its upper and lower parts in Squaloids, in *Scyllium* is extended caudad to the region of the ductus endolymphaticus. The dorsal part of this canal thus lies embedded in cartilage in the roof of the capsule.

The fossa parietalis differs from that in Squaloids. The dorsal part of the posterior semicircular canal only is visible in it but does not leave it by way a caudal opening on its way frontad. This depends upon the fact that the cartilage bridge below the canal is present in only the posterior part of the capsule. The deep incisure in the medial wall of the capsule in the region of the parietal fossa, in *Squalus* closed totally, in *Scyllium* remains open, contiguous with the vacuity enclosing the posterior semicircular canal. This incisure is also open in the adult skull (compare DE BEER). The cartilage bridge, later separating the incisure from the foramen of the endolymphatic duct, is a different structure in Squaloids and in *Scyllium*. In *Spinax* this bridge is built up between the roof of the braincase and that of the auditory capsule dorsal to the semicircular canal, whereas in *Scyllium* it extends from the roof

of the auditory capsule to its medial wall, passing ventrolateral to the semicircular canal. In the latter case the foramen shows mediad, in the former dorsad. There is, however, an inconsiderable remainder of the *Scyllium* bridge present in *Etmopterus* as a small cartilage rod not hitherto mentioned. The anterior branch of the acustic nerve is not embedded in the lateral wall of the auditory capsule even in the 90 mm stage.

On the medial side of the orbital cartilage is a process forming the first chondrified rudiment of the epiphysial bridge which in the 50 mm stage is present as an extremely slender bridge over the brain. It is, however, not bound to the epiphysis but lies behind it. There is no tectum orbitale in any of my stages but this ought to come later, continuing the tectum synoticum frontally as the space between this roof part and the epiphysial bridge is covered by cartilage in the adult skull.

The floor of the endolymphatic fossa is formed by a taenia medialis "growing out" frontad from the tectum posterius and joining secondarily the tectum synoticum, which is established somewhat later than the tectum posterius.

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The branchial skeleton (fig. 117) deviates somewhat from that of the 45 mm stage of DE BEER, but agrees with the figure given by GEGENBAUR of the visceral skeleton in *Scyllium catulus*. Between the basihyal and the first ceratobranchial a small independent hypobranchial I cartilage (fig. 117) has appeared. The hypobranchial I of DE BEER is the hypobranchial II corresponding to that of *Etmopterus*. In the 40 mm stage it is divided on the left side into two cartilages, but on the right side and in later stages it is single. The fifth ceratobranchial has caudally the incisure described by GEGENBAUR, lying in the same relation to the musculus adductor branchialis as the foramina of the other ceratobranchials. In this incisure the vena capitis lateralis bends down to the sinus venosus. A ligament runs out from the anterior upper corner of each epibranchial to the next frontal pharyngobranchial and inserts near its articulation with the epibranchial. The foremost ligament runs to the dorsal end of the hyomandibula, as described above. A blastematic nucleus in this ligament represents an interarcual cartilage, later chondrifying. The first pair of pharyngobranchials meets on the dorsal medial line.

MUSTELUS LAEVIS and GALEORHINUS MANAZO.

The development of the skull of *Mustelus* and *Galeorhinus* seems in essentials to correspond to that of *Scyllium*. Our material, however, being too scarce and insufficiently preserved for a full description, we have been forced to confine ourselves to the statement that these genera seem to behave much as *Scyllium*.

Heterodontus japonicus.

The development of the skull in *Heterodontus philippi* has been described by DE BEER (1924) in a paper based upon reconstructions of the skull of some stages. His description accounts for the development of the chondrified parts of the skull only, leaving out the blastemas in which the chondrification takes its origin. The present writer is not able to give any complete account of the *Heterodontus* development, as the material at disposal has been somewhat scarce and not well preserved for sections. Therefore only a few remarks will be given about some more interesting points of the development.

In a stage of 43 mm body length (fig. 119) the orbital cartilage is already broadly connected with the trabecular system, the acrochordal tissue and the parachordals. The polar cartilage is connected with the trabecula. The pituitary vein and the pseudobranchial artery are enclosed in young cartilage. The auditory capsule and the pila antotica are chondrifying. Behind the orbito-nasal vein (*o.n.v.*) the anterior sideplate is present as a membrane joining the trabecula with the orbital cartilage anterior to the eye and (apparently) posterior to the anterior cerebral vein (*a.c.v.*). In front of the orbito-nasal and anterior cerebral vein foramina lies the lamina orbitonasalis (*l.o.n.*). It is a very great lamella, dorsally in contact with the orbital cartilage. Ventrally it extends to the nasal sac, partly covering its sides and frontally the sides of the brain. Thus the long snout portion of the skull so characteristic of *Heterodontus* is built up principally of the orbitonasal lamina. The posteroventral part of the lamina orbitonasalis is formed by a thick blastematic mass which thins out by degrees frontally and ventrally. The nasal sac and the rudimentary secondary nasal capsule lie closely to the anteroventral (anterior) border of the prolonged part of the skull, so that the nasal capsule has already attained its terminal position.

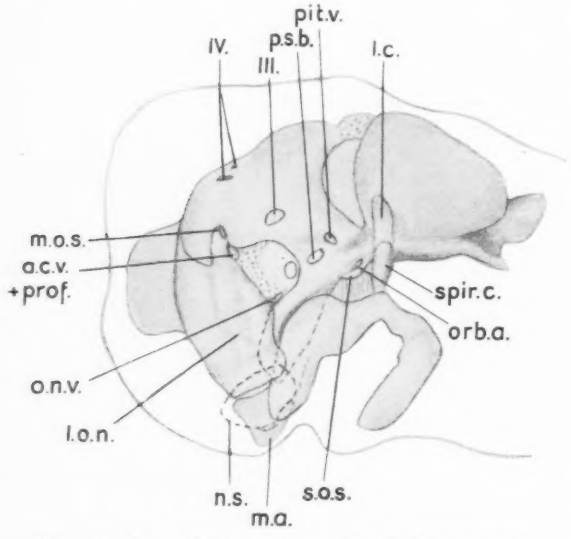

Fig. 119. *Heterodontus*. 43 mm. Skull. Reconstruction. Lateral aspect.

The anterior part of the dorsal eyebrow area in *Heterodontus* as in other sharks produces the epiphysial bridge, mesenchymatic in the 43 mm stage.

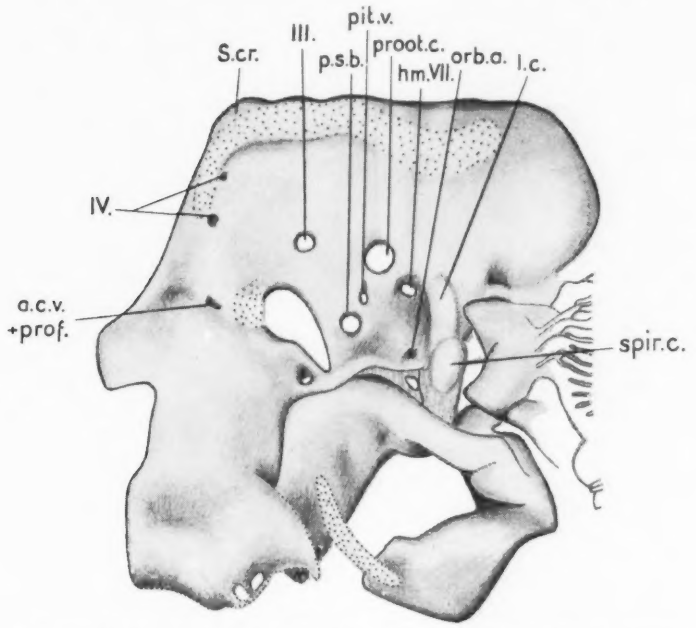

Fig. 120. *Heterodontus*. 54 mm. Skull. Reconstruction. Lateral aspect.

The 43 mm stage is already too old for determining the relations between orbital cartilage, polar cartilage, acrochordal tissue and parachordals, these parts already being completely fused to each other.

The medial area is developed as a high vertical lamella between the nasal sacs. This lamella lowers caudally and seems by degrees to form the trabecular commissure as in other sharks. The medial lamella caudally lies partly between the anterior ends of the palatoquadrates forming a symphysial tissue between them. In front the medial area enters between the nasal sacs forming the rudiment of the internasal septum.

A long and slender mesenchymatic postpituary commissure is present, and the precarotid commissure joins the polar cartilages in front of the carotids. This commissure is mesenchymatic but contains a medial centre of chondrification, which is apparently made up of the deep part of the medial area of this region. A subotical shelf, pierced by the orbital antery, is present.

The mandibular arch and its relations are of great interest. The palatoquadrates, exeepting their anterior tips, are connected with the trabecular system by a blastema. This blastema forms frontally a rather thick pad of tissue between the palatoquadrate and the trabecula. Posteriorly this pad flattens out dorso-ventrally to a lamella connecting the ventrolateral part of the polar cartilages and still more posteriorly the otical shelf rudiment (*s.o.s.*) with the palatoquadrate. In the shelf part chondrification has taken place so that the

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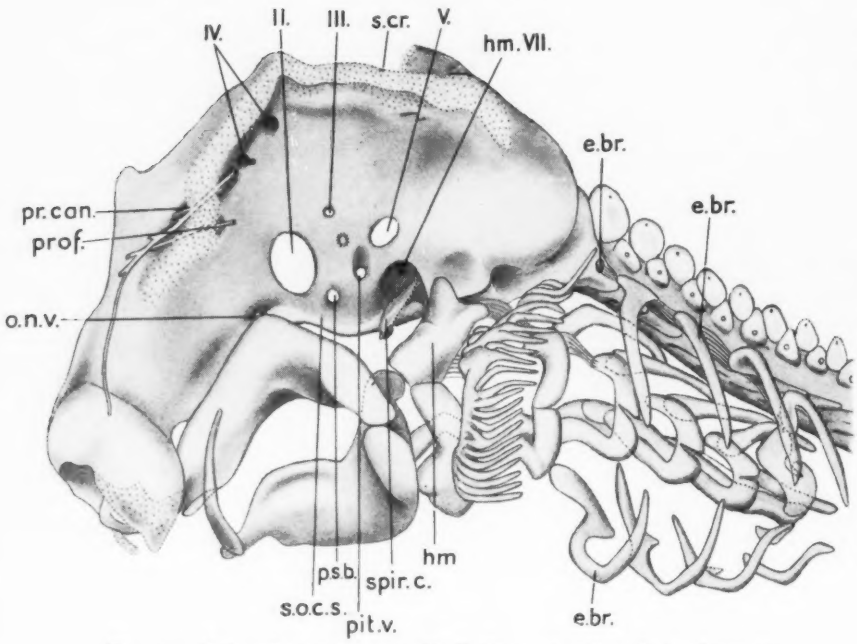

Fig. 121. *Heterodontus*. 62 mm. Skull. Reconstruction. Lateral aspect.

orbital artery is enclosed in a foramen between the otic capsule and the remainder of the blastematic lamina which in this region is also connected with the dorsal border of the palatoquadrate. Level with the anterior part of the auditory capsule, the blastematic lamella ends with a mesenchyma with which the lateral commissure rudiment of the otic capsule and the rudiment of the spiracular cartilages are continuous. The said mesenchyma, on the other hand, is connected with the palatoquadrate.

In our next stage (54 mm) (fig. 120) the definitive state of the skull is already attained principally. Therefore we cannot give any details about the development of the nasal capsule, the development of the taenia marginalis, etc., but must restrict ourselves to some remarks about those older stages investigated, referring to the figures given.

From the 54 mm stage compared witth that of 43 mm it is clearly understood that the rudiment of the epiphysial bridge has not changed in form but in size, its lateral parts now having merged without boundary with the snout region of the head on which the lamina orbitonasalis is no longer outlined. The anterior sideplate has chondrified behind the foramen of the orbitonasal vein. The nasal capsule is formed in connection with the terminal part of the snout. As in the preceding stage two trochlearis foramina are present in the orbital cartilage. The preorbital canal is not yet formed. The supraorbital crest (fig. 120, *s.cr.*) is forming. It extends caudad over the anterior

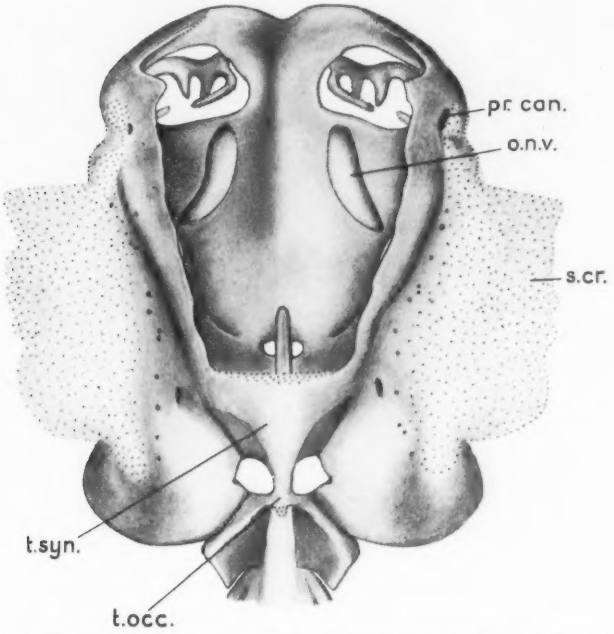

Fig. 122. *Heterodontus*. 62 mm. Skull. Reconstruction. Dorsal aspect.

part of the auditory capsule. That mesenchymatic lamella in the preceding stage joining the palatoquadrate with the neural cranium, in the 54 mm stage has chondrified medially and forms a subocular shelf. This crest as in the 43 mm stage is connected posteriorly with the always mesenchymatic "lateral commissure" (*l.c.*) and with the blastema of the spiracular cartilages (*spir.*).

In the 62 mm stage (figs. 121—124) adult conditions already seem to be established. The preorbital canal (figs. 121, 122, *pr.can.*) is formed but it can not be stated in what way. The frontal bordering crest of the orbita already hardly discernible in the preceding stage has now disappeared. The subocular shelf (figs. 121, 123, *s.o.c.s.*) is well chondrified medially and its caudal part no longer has a membranous connection with the palatoquadrate but ends in a diffuse mesenchymatic mass which extends to the palatoquadrate and to the spiracular cartilage. The "lateral commissure" of the preceding stage is now disorganized. Its components are still visible but they do not form any well outlined bridge lateral to the jugular vein and the hyomandibular nerve. In the 54 as well as the 62 mm stages the long and slender postpituitary commissure (fig. 124, *p.p.c.*) is quite chondrified and the precarotid commissure fused to the posterior margin of the trabecular plate.

Already in the 43 mm stage there is present a strong membranous tectum occipitale, but no tectum synoticum. In the 54 mm stage the tectum occipitale

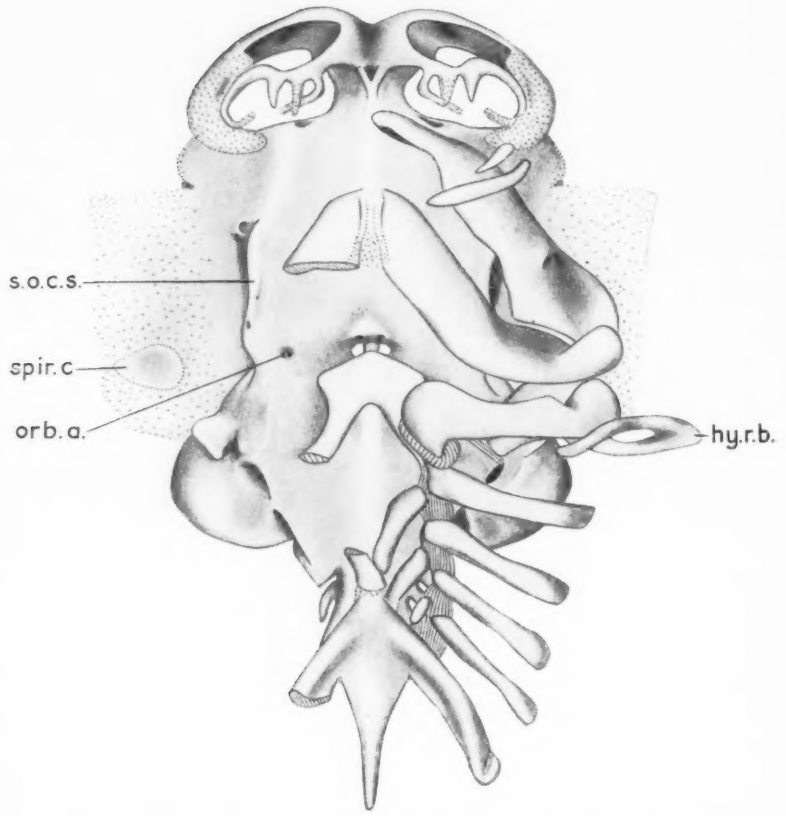

Fig. 123. *Heterodontus*. 62 mm. Skull. Reconstruction. Ventral aspect.

is about to chondrify laterally and the tectum synoticum is forming anterior to the endolymphatic duct. In the 62 mm stage the tectum occipitale (fig. 122, *t.occ.*) is chondrified excepting in the midline and the tectum synoticum (fig. 122, *t.syn.*) forms a complete but not fully chondrified roof above the brain in the auditory region. From the tectum synoticum a tectum mediale extends caudad to join the medial part of the tectum occipitale. In the orbital region the brain lies open except for the mesenchymatic layers covering it dorsally.

The auditory capsule demonstrates no mentionable differences to that of *Squalus* and *Etmopterus* and therefore will not be described.

The following remarks about visceral skeleton may be of interest.

The spiracular cartilage (fig. 121, *spir.c.*), which in the adult is a big bowl-shaped lamella, in the 62 mm stage is composed of five short, parallel and caudally confluent rods of which three issue anteriorly from a common basal part. Frontally the rods lie between the pseudobranchial arteries, caudally

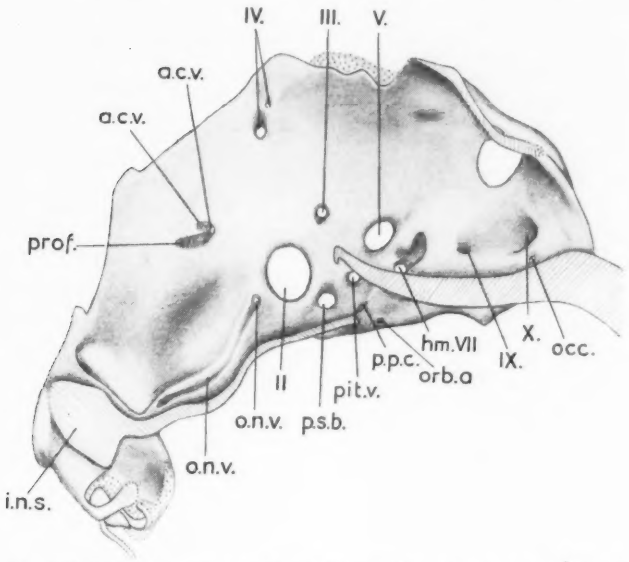

Fig. 124. *Heterodontus*. 62 mm. Longitudinal section of the skull. Reconstruction.

they form a plate dorsal to the pseudobranch. The large spiracular cartilage of the adult is thus composed of a number of branchial rays.

The hyoid arch behaves as in *Squalus* and *Etmopterus* and *Scyllium*. All the ceratohyal branchial rays are fused to each other basally so that their bases form a "pseudohyoid" as described in rays by KRIVETSKI (1917).

The branchial basket agrees in principle with that of other sharks. Five dorsal and four ventral extrabranchials are present, the first dorsal, however, being rudimentary.

DEVELOPMENT OF THE SKULL IN RAYS.

In the literature dealing with the development of the skull in elasmobranch fishes there are only a few researches on the rays. According to DE BEER (1926) very little of interest would be gained from such an investigation. But as the systematical position of the rays in relation to the sharks has been discussed from the point of wiew of a possible polyphyletic development of the selachians, a detailed study of the development of the skull of rays would undoubtedly throw some light upon this phylogenetical question. Since the work of PARKER (1897) dealing with the cranial development of *Raja*, only scattered notes have been published on the subject. In 1926 DE BEER described a 24 mm stage of *Torpedo marmorata* and in 1926 (*a*) he gave some account of an embryo of *Raja blanda*. After that came a 12 cm specimen of *Raja*

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clavata, investigated by HOFFMAN, and a 24 mm stage and of *Torpedo ocellata* published by DE BEER (1937).— This completes the list of principal works on the cranial development in rays. Investigations into the structure of the hyoid arch have been published by DOHRN (1886), KRIVETSKI (1917) and DE BEER (1932).

RAJA CLAVATA.

Raja clavata, stage 38 mm (39 days old).

In spite of the great length of the embryo, the rudiment of the skull is not very far advanced. The long tail of the embryo accounts for this condition. Chondrification has begun in the parachordals only. The notochord has a hooklike anterior tip. The parachordals are, as in *Squalus*, thickened along the notochord. They thin out laterally and have blastematic lateral parts. In the anterior part of the auditory capsule region their lateral border, a mesenchymatic lamella, seems to bend up between the brain and the auditory vesicle, forming the oblong rudiment of the processus dorsalis (medial wall of the capsule)[1]. The central nervous system in the otical region thus rests in a blastematic furrow, of which the floor is formed by the notochord and the parachordals. The basiotic lamina, though present, consists of a diffuse mesenchyma only. Behind the auditory vesicle the borders of the furrow arise to form the rudiments of the occipital columns (fig. 125, *o.c.*). Behind these the parachordals continue as a ridge on each side of the notochord. These ridges are already present in a 21.5 mm stage, where the parachordals extend from the level of the spiracular canal to the level of the last branchial cleft.

Rather large but somewhat diffuse rudiments of the polar cartilages (fig. 125, *p.b.*) are present, lying ventrolateral to the anterior tip of the parachordals. They are connected with the lateral part of the very diffuse acrochordal tissue (*acr.*) underlying the notochord. They are still free from the rudiments of the trabeculae.

The trabeculae lie closely to the future ventral part of the fore-and 'tweenbrain, topographically below the anterior tip of the parachordals (*p.c.*). They form a wide angle (more than 90°) against the parachordals. The trabeculae (*trab.*) are represented by two cell laminas, one on each side, covering the basal part of the fore-and 'tweenbrain. Medially they are connected by the deep part of the medial area (*m.a.*) which apparently forms the long trabecular commissure. The medial area enters caudally between the antero-ventral tips of the palatoquadrates; frontally it extends between the nasal areas a long distance anterior to the tips of the trabeculae. Somewhat behind its middle

[1] Probably, in *Raja* as in other selachians the bent-up part is connected with the lamina basiotica, as there is a distinct limit between this part and the parachordal.

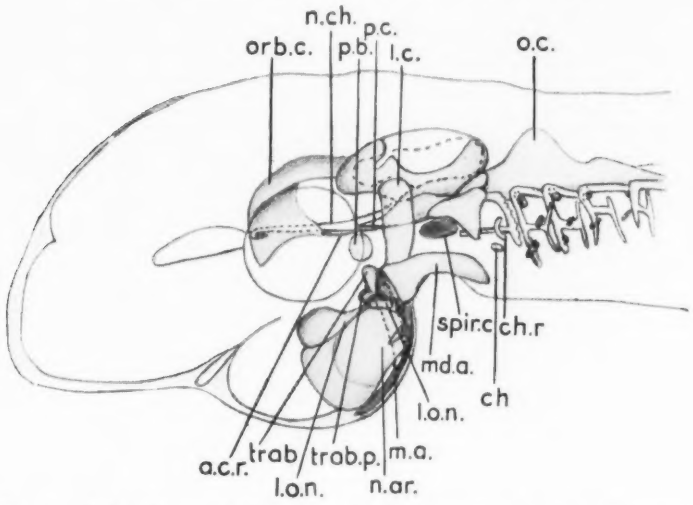

Fig. 125. *Raja*. 38 mm. Skull. spir.c, spiracle. Reconstruction. Lateral aspect.

part the trabecula has a short diffusely outlined, frontally directed, process (fig. 125, *trab.p.*) at the base of which is inserted a part of the obliquus inferior muscle of the eye. This process is the rudiment of the "anterior sideplate". Dorsofrontal to the nasal area on each side is a rather large mass of cells. Caudally this mass (*l.o.n.*) becomes narrower and very obsolete, more caudally still widening to a small lamella connected with the trabecula. This cell mass (anterior and posterior part) represents the orbitonasal lamina. The nasal area (*n.ar.*) is very large, extending far frontad.

The orbital cartilage (fig. 125, *orb.c.*) is represented by a very diffuse mesenchyma lying in front of the auditory capsule and connected with it through a blastematic taenia marginalis. The orbital blastema extends dorsally to the skin of the supraorbital area; ventrally it reaches down between the eye and the brain. It is connected by strands of mesenchyma with the acrochordal bed of the anterior part of the notochord.

The auditory capsule is diffusely outlined medially and dorsally. Ventrolaterally a denser mesenchyma is present. Frontally it surrounds the anterior end of the auditory vesicle. This mesenchyma has an anterior and a posterior portion (anterior and posterior cartilage of the auditory capsule).

The mandibular arch (fig. 125, *md.a.*) on each side consists of a single blastematic piece, whereof the palatoquadrate part is connected frontally with the trabecula by a lamella, which at the lateral side of the trabecula widens to a thick pad of mesenchyma, which is confluent also with the trabecula. It is not possible to tell at this stage whether this pad is to be considered a process of the trabecula or a part of the trabeculo-palatoquadrate lamella. Into this process and partly also on the anterior (dorsal) margin of the

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trabecula (at the basis of the sideplate) is inserted the rudiment of the obliquus inferior muscle of the eye. In this respect the process behaves as the lateral process of the trabecula in *Squalus*, and therefor the similar process in *Raja* should be considered a part of the trabecula. The future development of the process in *Raja*, however, indicates a certain independence of it as will be demonstrated in later stages of development.

In the present stage of development the palatine process is represented by a blastematic down-and-inwards directed process, including the rudiment of the process proper as well as the teeth blastema. At the upper margin of the palatoquadrate issues a great blastematic mass. It extends dorsad outside the facialis ganglion and the jugular vein and contains the rudiment of the "lateral commissure" (*l.c.*) as well as of the prespiracular cartilage. This blastema includes also a portion lying lateral to the mandibular muscle layer and a more ventral portion extending to the skin. The former of these portions is the rudiment of a lateral "ray"—the bed of the tendon of the musculus levator rostri—,the latter the extrapalatoquadrate. In a 21.5 mm stage the mass is shorter, its connection with the palatoquadrate stronger and its different parts more confluent.

In the hyoid arch is a big dorsal prochondrial piece, the rudiment of the hyomandibula. This rudiment is broadened dorsally to a longitudinal blastematic plate closely adhering to the auditory capsule. This blastema is less dense than that of the remainder of the hyomandibula. As will be pointed out later, it probably represents the pharyngohyal element of the hyoid arch. To the hyoid arch belongs, further, an inconsiderable ventral blastema, corresponding to a ceratohyal element (*c.h.*). Lateral to the afferent pseudobranchial artery, running lateral to the lower part of the hyomandibular, two basally fused rays (*ch.r.*) are already established. These form the rudiment of the "pseudohyal" with two of its rays. Each following visceral arch (fig. 125) consists of at least two well-separated blastematic elements. These decrease caudad and their parts become more widely separated. As is seen from the reconstructions, during their first development they are related to the branchial arteries. The transversal commissures above and below the branchial clefts are not yet established. The connection between the dorsal aorta and the inner carotid artery has disappeared and the pseudobranchial artery is formed. Medial to each branch of the aorta, bending down in the arch, lies the dorsal element of each branchial arch. The ventral parts are situated dorsal to the afferent branchial artery, extending to or towards the blood vessel connecting the anterior and posterior capillary system of each arch. A third blastema occurs lateral to the said connecting vessel, at least in the first and second branchial arch. It extends laterally towards the capillaries and must represent a first branchial ray, independent of origin.

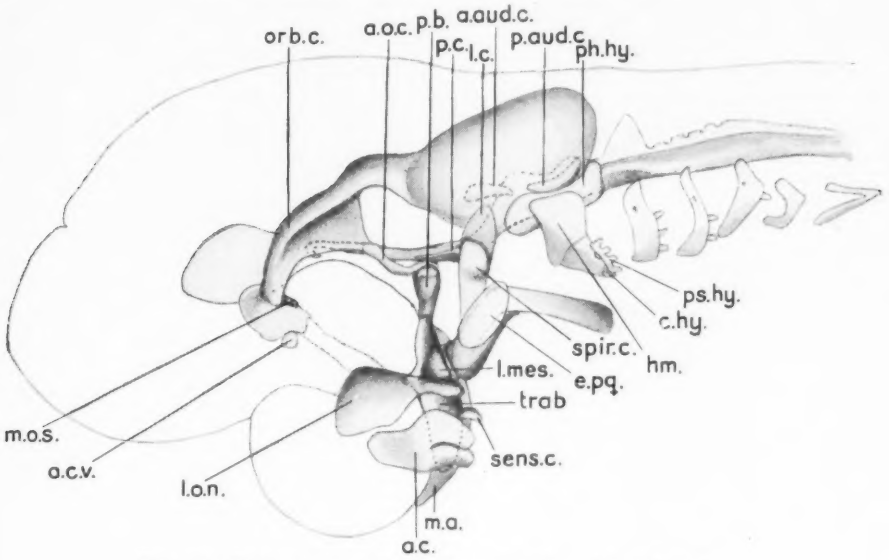

Fig. 126. *Raja*. 40 mm. Skull. Reconstruction. Lateral aspect.

Raja clavata, stage 40 mm.

The parachordal plates (fig. 127, *p.c.*) which are the only chondrified parts of the skull, are united below the notochord in almost the entire skull. Frontally they are pointed, caudally broadening considerably. An indentation (fig. 126) on the upper border of the processus dorsalis, through which the glossopharyngeus runs, shows that the long processus dorsalis in *Raja* consists of an anterior process (fig. 126), corresponding to that in sharks, and a posterior one. Between the latter and the occipital column runs the vagus nerve. The lamina basiotica extends laterad below the acoustic vesicle establishing the anterior (fig. 127, *a.bc.c.*) and posterior (*p.bc.c.*) basicapsular commissures. Beyond these lie two independent blastematic discs, the chondrifying centres of the auditory capsule. The anterior of these is an obliquely vertical plate lateral to the auditory nerve and to the rather undifferentiated auditory vesicle, and medial to the ramus hyomandibularis VII. It corresponds to the laterally raised part of the anterior auditory capsule cartilage in the sharks. The posterior rudiment lies like a bowl below the already differentiated recessus utricularis, and thus forms part of the floor of the future capsule. Against it the hyomandibula articulates, and above the posterior part of it runs the glossopharyngeal nerve. It thus corresponds to the posterior auditory cartilage in sharks. On the outside of the occipital column, below the vagus nerve, a ridge is formed on a level with the lamina basiotica. The occipital column is not pierced by any occipital nerve. From the basal band of the vertebral column a blastematic band follows the spinal

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cord on each side. Through notches in its border run the ventral spinal roots (fig. 126).

In front of the parachordals the notochord rests upon a bed of mesenchymatic tissue, constituting the acrochordal tissue (fig. 127, *acr.*). This bed runs out laterally in thin lamellae, which are connected on each side with the rudiments of the antotic cartilage (figs. 126, 127, *a.o.c.*). In the preceding stage these rudiments are perhaps represented by condensations of the extreme lateral parts of the acrochordal tissue, but these condensations are so indistinct that it is not possible to tell whether they belong to the acrochordal tissue or are independently formed. In the 40 mm stage, however, the antotic rudiments are distinct, but their origin could not be determined with any certainly. The antotic cartilages (*a.o.c.*) of the 40 mm stage are mesenchymatic rods diverging frontad, and connecting in front with a less advanced orbital lamella (*orb.c.*) consisting of a superficial thick part lying in the supraorbital area and a more or less vertical part entering between the eye and the brain. The superficial part of the orbital cartilage is connected caudally with the primary auditory capsule rudiment, forming a taenia marginalis. Frontally the orbital cartilage rudiment meets a blastema into which the obliquus superior (fig. 126, *m.o.s.*) muscle is inserted. This blastema forms the upper end of the future anterior boundary of the orbit. The posterior end of the antotic cartilage rudiment connects with the lateral border of the parachordal and separates the parachordal from the rudiment of the polar cartilage (figs. 126, 127, *p.b.*), of which the dorsal border fuses with the antotic cartilage (acrochordal tissue?), whereas its ventral (anterior) part is connected with the trabecula. The trabeculae (*trab.*) are broad prochondrial plates almost reaching one another in the midline, where the medial area (*m.a.*) forms a connecting link between them. On the anterior (dorsal) border of the trabecula, a little behind its mid-point, a short process represents the ventral part of the anterior sideplate, and lateral to this process a mass of mesenchyma represents the posterior part of the lamina orbitonasalis (*l.o.n.*). The orbitonasal vein passes dorsal to this lamina and lateral to the anterior sideplate i.e. between the lamina and the sideplate.

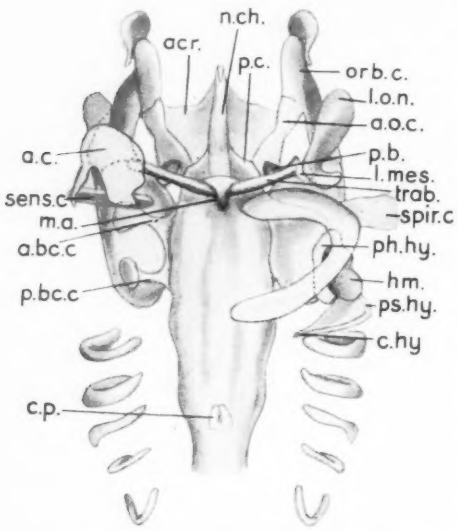

Fig. 127. *Raja*. 40 mm. Skull. Reconstruction. Ventral aspect.

The olfactory organs lie lateral to the anterior half of the trabeculae. They are surrounded by a primary nasal capsule of mesenchyma, of which the rudiment of the annular cartilage (figs. 126, 127, *a.c.*) is the superficial part. The rostral part of the infraorbital sensory canal proceeds to the caudal border of the nasal sac. The canal is deeply sunken here, on its upper side covered by its mesenchymatic layer. This layer will later chondrify and form the socalled "labial cartilage" of *Raja* (*sens.c.*). Frontally the nasal mesenchyma is in contact with the anterior part of the lamina orbitonasalis. It subsequently will form the dorsal part of the future nasal capsule.

The palatoquadrate portion of the mandibular arch, is, as in the preceding stage, connected with a thick mesenchymatic mass (figs. 126, 127, *l.mes.*) lying on the outside of the trabecula and continuous with that structure. Into this mass is now inserted the obliquus inferior muscle of the eye. The palatine part of the palatoquadrate is well developed and seems to be to a certain extent delimited from the rest of the arch, but not from its superficial teeth blastema. On the outside the palatoquadrate portion carries a large blastema ("extrapalatoquadrate") (fig. 126, *e.pq.*), extending to the epithelium. This blastema will later on be absorbed in the development of the dorsolateral muscular crista or process of the palatoquadrate. It extends beyond the locus of the future mandibular articulation. On the dorsal border of the palatoquadrate portion the blastema of the spiracular cartilages has differentiated into a medial portion, the rudiment of the lateral commissure (*l.c.*), and a lateral part, the rudiment of the spiracular cartilage (*spir.c.*) proper. To this complex also belong the rudiment of a lateral "ray" forming the bed of the tendon of musculus levator rostri. (See stage 47 mm).

The hyoid arch consists of three elements, viz. a pharyngohyal, an epihyal and a ceratohyal. The pharyngohyal (figs. 126, 127, *ph.hy*) consists of a mesenchyma covering the ventro-lateral surface of the auditory capsule. Frontally it extends to the level of the anterior auditory cartilage, caudally to the occipital column. The caudal end of the blastema bends up on the lateral side of the jugular vein. Later the pharyngohyal will fuse with the auditory capsule, forming the "Rochenfortsatz" of HOFFMANN. The epihyal or hyomandibula (*hm.*) is a broad plate of dense prochondrial tissue still continuous with the pharyngohyal rudiment. From its ventral border a thin lamella issues which connects ventromedially with the very insignificant rudiment of the ceratohyal. This rudiment is fused with the ventromedial end of the pseudohyal (*ps.hy.*) of KRIVETSKI, the nature of which was described in the preceding stage. There are now four rays on the pseudohyal. The "pseudohyal" is not the "pseudohyal" of KRIVETSKI (1917) and DE BEER (1926) and not the ceratohyal, as stated by EDGEWORTH, but it is the "pseudohyal" + the ceratohyal.

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In all branchial arches the dorsal and ventral elements have fused. Each arch is thus formed like a slightly curved mesenchymatic rod. In the dorsal parts of these rods there are foramina for nerves belonging to the vagus system, running to the adductor muscles. In the ventral parts of the arches no foramina are formed, or at least they are closed very early. The number of rays has increased in the two anterior arches.

At the level of the third branchial arch the first rudiments of the copular plate (fig. 127, *c.p.*) have appeared in the medial line. They consist of two short longitudinal blastematic rods lying closely together.

Raja clavata, stage 43 mm.

The 43 mm stage is of some importance as it forms the connecting link between the 40 mm and the 46 and 47 mm stages, in such a manner that structures of the earlier (younger) stage, the future development of which could not be foreseen with certainty through the 43 mm stage can be determined as to their future and outlined in the 46 and 47 mm stage, their conditions there being more advanced.

Both the anterior and the posterior auditory capsule cartilages are connected with the lamina basiotica. The posterior has become enlarged caudally, reaching the region of the occipital column and forming a broad plate, dorsal to which runs the glossopharyngeal nerve.

Two slender blastematic commissures, the postpituitary and the precarotid, connect the polar cartilages with one another. The polar cartilage is fused with the trabecula (fig. 128). The trabeculae are connected in the midline by means of the high lamella of the medial area (*m.a.*), which runs out anteriorly in an internasal and rostral process. The trabecular plate is thus strongly keeled medially. The medial keel continues in front of the trabeculae. In this part the deep portion of the medial area broadens and forms o bowl, in which the ventral part of the forebrain rests, thus constituting part of the primary ventral cranial wall. This pretrabecular part is the rudiment of the future rostrum (fig. 128, *m.a.*), which in this stage exclusively forms the above mentioned part of the cranial wall.

The "anterior sideplate" of the 43 mm stage is connected with the upper rudiment (of the 40 mm stage) through a blastematic band, and the obliquus superior muscle is inserted into its dorsal end. Thus the orbita is delimited anteriorly. The anterior cerebral vein, however, lies *anterior* to the "sideplate".

Laterally to the trabecula the independent blastematic rudiment of the lamina orbitonosalis (*l.o.n.*) is found between the eye and the nasal sac. It extends laterally to the posterior margin of the nasal sac (*n.s.*). The orbitonasal vein runs between the orbitonasal lamina and the basal part of the "anterior sideplate". The position of the rudiment of the lamina orbitonasalis

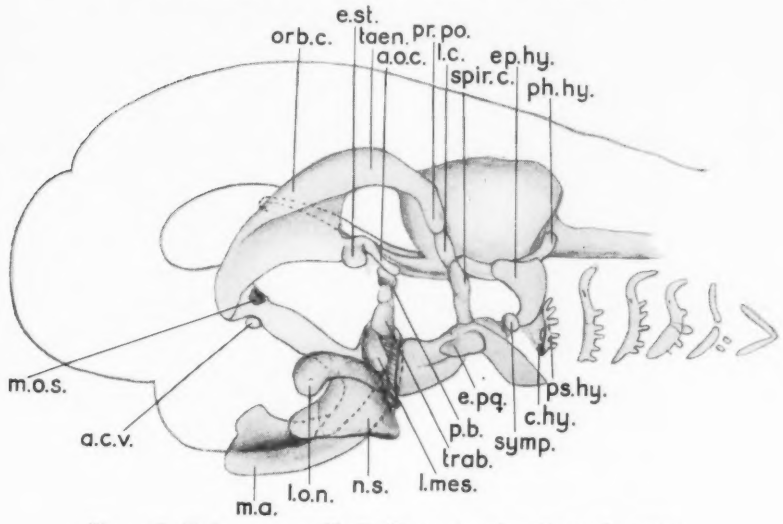

Fig. 128. *Raja*. 43 mm. Skull. Reconstruction. Lateral aspect.

in relation to the orbitonasal vein signifies that it corresponds to the lamina orbitonasalis in sharks.

The rudiment of the orbital cartilage (*orb.c.*) has not changed to any great extent since the 40 mm stage. At the frontal end of its antotic portion (*a.o.c.*), the rudiment of the eyestalk (*e.st.*) has arisen out of the premandibular somite, the cavity of which has been filled in with mesenchymatic cells at least partly derived from the walls of the cavity. The dorsal part of the rudiment of the orbital cartilage extends caudally to the lateral surface of the rudiment of the auditory capsule and there forms a processus postorbitalis (fig. 128, *pr.po.*).

The nasal sac is surrounded by the primary nasal capsule, of which the rudiment of the annular cartilage is differentiated. The anterior wall of this capsule is very thick, owing to the fact that a fairly large mass of mesenchymatic cells belonging to the eyebrow area is located in immediate contact with the capsule. In fact, there is no distinct line of demarcation between this cell mass and the capsule. This cell mass was already present in the 38 and 40 mm stages, but was not mentioned there (indicated, however, in figs. 125 and 126).

In the mandibular arch the palatoquadrate is about to separate from the mandibular portion. The palatoquadrate has frontally moved somewhat away from the trabecula, and consequently the membrane connecting it with the mesenchymatic process (figs. 128, 129, *l.mes.*) of the trabecula has lengthened slightly. The above mentioned process of the trabecula with the eye muscle is partly about to sever its connecting with the trabecula, its frontal (dorsal) border being still connected with the trabecula, its caudal

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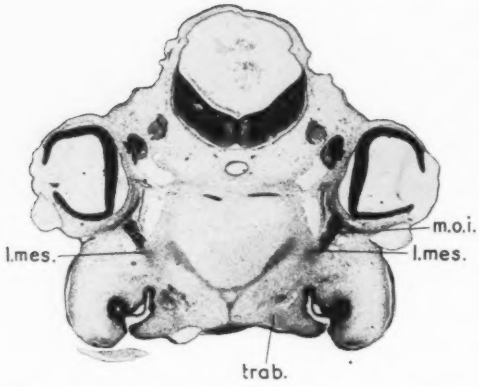

Fig. 129. *Raja*. 43 mm. Transverse section through the region of the lateral mesoderm of the trabecula.

(ventral) border having moved a considerable distance from it. The lateral appendix of the palatoquadrate portion—the "extrapalatoquadrate"—is now destined to become a muscular crista on the palatoquadrate. Caudally, this portion extends above the future mandibular articulation. The spiracular cartilage (*spir.c.*) and the "lateral commissure" (*l.c.*) rudiments are the same as in the preceding stage, the latter, however, joins the postorbital process dorsally (*pr.po.*).

The hyomandibula, is composed of a dorsal pharyngeal (*ph.hy.*) and a ventral epal element (*ep.hy.*) as in the preceding stage. The ventral end of the epal element is bent frontad towards the mandibular articulation, to which it is joined by means of an interposed rounded mesenchymatic rudiment, a "symplecticum" (*symp.*), which will be discussed later.

The insignificant ceratohyal (*c.hy.*) is fused with the ventromedial end of the pseudohyoid (*ps.hy.*), which has become enlarged by the formation of new rays.

The initial chondrification of the branchial arches again divides each of them into two parts, viz., the pharyngo-epi- and the cerato-hypobranchials. From at least the second and the third of the former extend posteriorly directed dorsal processes, corresponding to the future pharyngobranchials. These do not form independently in *Raja*. All arches, with the exception of the most caudal, have rays, especially on their ceratobranchial parts. The two elements of the copular plate have fused on to a triangular plate running out anteriorly in two cylindrical rods.

Raja clavata, stage 46 mm.

In the floor of the auditory capsule there remains only a small perforation: a rudimentary fenestra basicapsularis (figs. 131, 132, *f.bc.*). The chondrifying part of the lateral wall of the capsule rises from the floor higher in the anterior and posterior part of the capsule than in its medium part. In the posterior part a foramen for the exit of the glossopharyngeal nerve (figs. 131, *IX.*) has formed. Below this nerve a prochondrial rod is inserted, which bends up on the lateral side of the nerve and the vena capitis lateralis (fig. 131, *v. jug.*). The medial wall of the capsule is relatively well developed. It is pierced by the acoustic (*VIII.*) and glossopharyngeal (*IX.*) nerves. The pro-

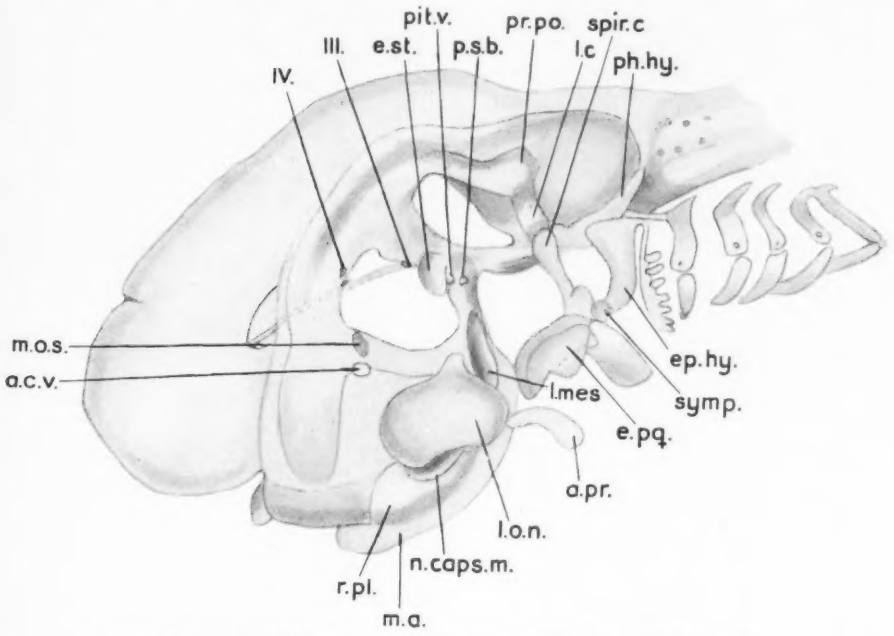

Fig. 130. *Raja*. 46 mm. Skull. Reconstruction. Lateral aspect.

cessus dorsalis (fig. 131, *pr.d.*) forms the medial wall of the auditory capsule, also behind the glossopharyngeal foramen. No specially developed cartilage of KÄLLBERG is present. The course of the vagus nerve (fig. 131, *X.*) of this stage is remarkable in *Raja,* as this nerve, like the glossopharyngeal, runs through the auditory capsule. Regularly the nerve should go between the occipital column and the auditory capsule. The otic capsule, however, bulges out posteriorly. Its postero-medial wall thus lies close to the occipital column. A transverse section of it therefore seems to be two-layered. The vagus nerve runs caudad in a canal between these two layers. Caudally the capsular part of the two-layered wall is very thin, so that practically the column itself alone forms the wall. The vagus nerve is then separated from the cavity of the capsule by only a thin layer. In later stages this layer disappears and then the vagus nerve runs over the posterior portion of the floor of the capsule, leaving it through its posterior part. The articulation between the skull and the vertebral column has become established through the forming of two frontad converging fissures, which separate a posteriorly concave frontal part of the parachordals from an anteriorly convex posterior portion. The vertebral column thus enters like a wedge between the caudad diverging parachordal plates (fig. 131). As the fissure mentioned just above is somewhat obliquely located, the ventrofrontal side of the wedge rests upon the parachordal plate. Behind the occipital column follows the anterior section

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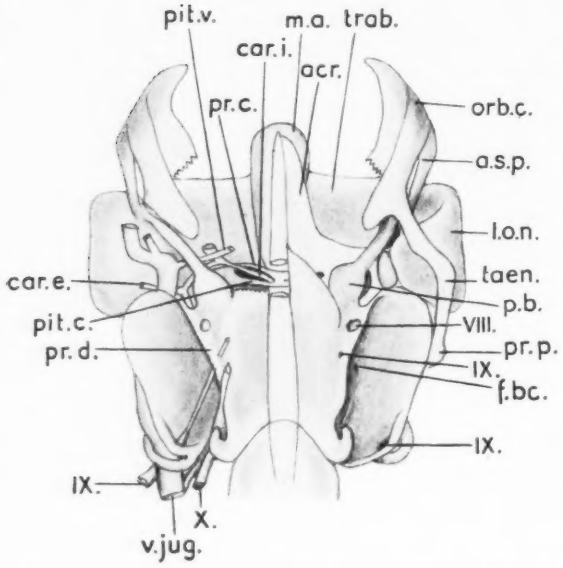

Fig. 131. *Raja*. 46 mm. Skull. Reconstruction. Dorsal aspect.

of the vertebral column, pierced by ventral as well as by dorsal spinal roots. In this section no separate arches are formed as in sharks, but it chondrifies, as typically in rays, in one piece. Along its lateral side a blastematic longitudinal ridge has formed, corresponding to the lateral vertebral processes in adult rays. In later stage the auditory capsule—caudally lengthened—articulates against the outside of the vertebral column. The articular process ultimately (70 mm stage) reaches the lateral ridge of the vertebral column, against the frontolateral side of which it ends as a vertical condyle.

In the anterior parts of the skull considerable development has taken place. The orbital cartilage has fused completely with the antotical (fig. 130) and the latter with the parachordal some distance caudally to its tip, as in sharks. The pituitary vein and the efferent pseudobranchial artery have been enclosed in foramina formed almost as in the sharks. Immediately in front of the pituitary foramen the rudiment of the eyestalk (fig. 130,*c.st.*) is inserted on the outside of the antotic cartilage, as in sharks.

At the medial side of the polar cartilages a postpituitary and a praecarotid commissure are well established (fig. 131, *pr.c.*, *pit.c.*). They issue close behind the fusion of the paired carotids, and between the arteries the two commissures are connected with a narrow medial blastema. Through this arrangement the carotids become two foramina, lying close together. The postpituitary commissure is well separated from the parachordal plate.

The orbital cartilage in *Raja* is formed dorsal to the trochlear as well as to the oculomotor nerves (fig. 130). It consists of a posterior thickened crestlike part caudally running out in the still blastematic taenia marginalis and in a processus postorbitalis (*pr.po.*). An anterior portion of the orbital cartilage embraces the forebrain hemispheres. It comes down towards the rostral plate in front of the "anterior sideplate". The supraorbital crest is formed from the dorsal eyebrow area. From about the middle of the postero-inferior

margin of the orbital cartilage in the 40 mm stage there issues a process, into which the musculus obliquus superior (fig. 130, *m.o.s.*) is inserted. This process in the 43 and 46 mm stages ventrally is continued by the "anterior sideplate". Lateral to it runs the orbitonasal vein. *Anterior* to the upper end of the sideplate lies the foramen for the anterior cerebral vein (*a.c.v.*).

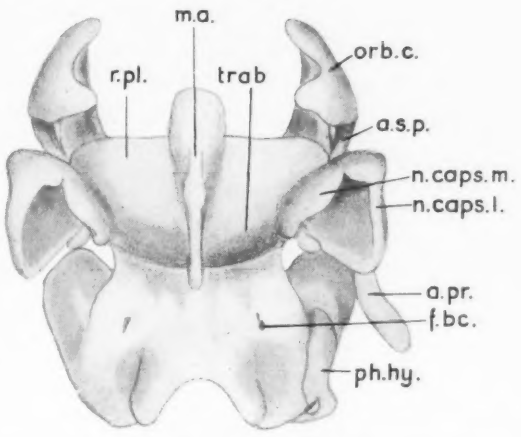

Fig. 132. *Raja*. 46 mm. Skull. Reconstruction. Ventral aspect.

The medial area (figs. 130—132, *m.a.*), well outlined in the preceding stage, forms the medial part of the trabecular plate. The hypophysial fenestra is a broad opening between the basal parts of the trabeculae. It is not seen in the reconstruction owing to the wide angle between the parachordals and the trabeculae. The lamina orbitonasalis of the 46 mm stage immediately behind the nasal sac has a blastematic continuation forming the rudiment of the "antorbital cartilage" ("Flossenträgerknorpel") (fig. 130, 132, *a.pr.*).

In the 46 mm stage the essentials of the secondary nasal capsule are formed. There are present a lateral (figs. 130, *l.o.n.*, 132, *n.caps.l.*) and a medial (*n.caps.m.*) rudiment of the nasal capsule. The lateral cartilage consists of two parts, a dorsal and a ventral. The dorsal part corresponds to the rudiment described in the preceding as the lamina orbitonasalis. To the ventral border of this rudiment is atached the ventral rudiment. It consists of a fairly thin lamella of mesenchymatic cells covering the lateral surface of the nasal sac. The ventral (medial) rudiment of the nasal capsule (fig. 132, *n.caps.m.*) has formed along the lateral border of the rostral plate anteriorly and extends caudally along the upper (lateral) border of the trabecular plate. This part of the nasal capsule is foreshadowed in the 43 mm stage by an indistinct oblong group of mesenchymatic cells. Thus this part is formed in situ. The dorsal part of the lateral wall of the capsule is connected with the trabecula at the basis of the "anterior sideplate". In the angle between the trabecula and the lateral nasal cartilage one of the musculi levatores labii superioris is inserted into the capsule (lamina orbitonasalis). The lateral process (fig. 130, *l.mcs.*) of the trabecula on which the obliquus inferior muscle of the eye is inserted is as in the preceding stage.

The mandibular arch is divided into the palatoquadrate and the mechelian cartilage, but in other respects it is as in the preceding stage. The rudiment

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of the spiracular cartilage and that of the lateral commissure are as before. The hyomandibula (epihyal) has dorsally a caudally directed process, which connects it with the upper end of the pseudohyoid (fig. 130). The pharyngohyal is, as in the preceding stage, mesenchymatic, lying closely to the ventrolateral side of the otic capsule, and is fused on to it. Its posterior end bends upwards and embraces the lateral side of the jugular vein and the glossopharyngeal nerve, which have thus become enclosed by a skeletal ring (figs. 130—132). An already tendinous cord, which is inserted caudally into the upper end of the epibranchial part of the first branchial arch (fig. 130), issues from the ventro-caudal corner of the pharyngohyal rudiment. This cord corresponds to the pharyngo-epibranchial tendons of the branchial arches. The ceratohyal is incorporated with the lower part of the pseudohyoid. The lower end of the hyomandibula is bent frontad towards the mandibular articulation but reaches the latter only by means of *an independent* spherical *blastema* (fig. 130, *symp.*), well outlined at this stage.

The ceratobranchials have blastematic hypobranchial processes. The first hypobranchial process is very slender and reaches a small blastema situated in the midline on a level with the mandibular symphysis but more dorsally. The bridge thus developed was called by GEGENBAUR (1892) the basihyal and RABINERSON (1925) found it to be composed of the two hypobranchials I fused in the midline. Apparently, however, it also contains a first basibranchial. The anterior processes of the copular plate now diverge towards the hypobranchials II, of which they represent the medial parts. The third hypobranchial is connected with the fourth arch.

Raja clavata, stage 47 mm.

This stage is of interest from two points of view. It is somewhat more advanced than the preceding and therefore structures that were already present but indistinct in the 46 mm stage have in the 47 mm stage become more distinct; and new details have arisen, and fusion have taken place.

The outline of the skull is about as in the 46 mm stage, but details have altered. The anterior part of the orbital cartilage has grown out both considerably frontally and frontoventrally (fig. 133). The rostrum is longer and the trabecular plate has become extended frontad owing to the deep part of the medial area (*m.a.*) being added to the frontal part of the trabeculae (fig. 135). The proximal part of the trabecula + polar cartilage is joined and fused with the proximal part of the pila antotica, which is connected with the parachordal. The fusion between the polar cartilage and the pila antotica has taken place wherewith the efferent pseudobranchial artery as well as the pituitary vein have become surrounded by cartilage (fig. 133). The connection between the trabecula and the orbital cartilage in front of the eye is

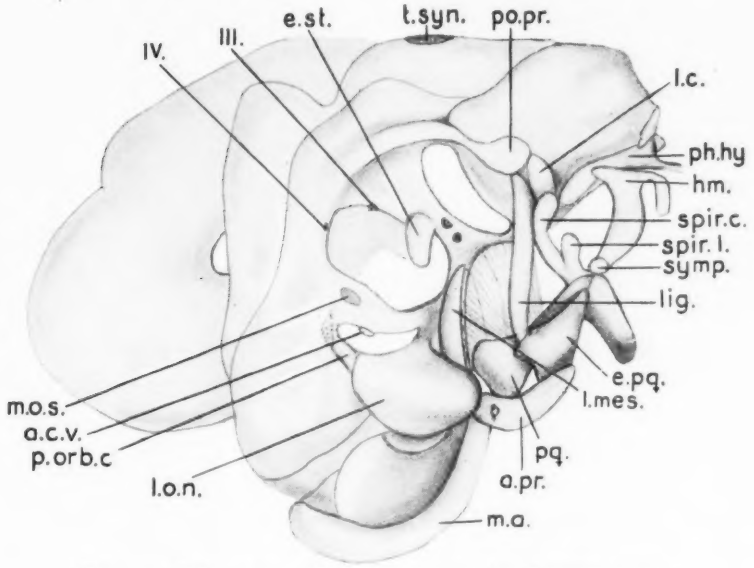

Fig. 133. *Raja*. 47 mm. Skull. Reconstruction. Lateral aspect.

fully established. The foramen of the anterior cerebral vein lies *in front* of this connection (anterior sideplate), not, as in most sharks, posterior to it.

The nasal capsule rudiment is as in the 46 mm stage, but the anterodorsal corner of the dorsal wall rudiment (fig. 133, *p.orb.c.*) is connected by a blastematic process with the orbital cartilage anterior to the sideplate connection, the foramen of the anterior cerebral vein lying between the two connections. The process lies laterally to the nervus ophthalmicus superficialis VII and the n. ophthalmicus profundus, and thus forms the side-wall of the preorbital canal (fig. 133, *p.orb.c.*). The process thus corresponds topographically to the preorbital cartilage in *Squalus* and *Etmopterus*. It also corresponds to this cartilage genetically, as it developes from the anterior part of the eyebrow area, as does the cartilage in the mentioned genera.

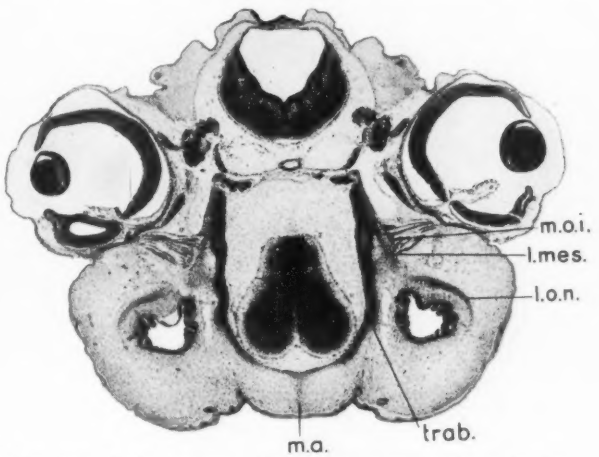

Fig. 134. *Raja*. 47 mm. Transverse section through the region of the lateral mesenchyma of the trabecula.

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The lateral mesenchyma (fig. 133, 134, *l.mes.*) of the trabecula has extended along its lateral side. It is connected with the trabecula with its anterior (dorsal) margin. Its posterior (ventral) margin is removed from the trabecula. At the posterolateral border the nasal capsule carries the mesenchymatic rudiment of the antorbital cartilage (fig. 133, *a.pr.*, 135).

The auditory capsule has continued its development more and now has an almost complete lateral wall. The medial wall is also more or less complete, pierced by the *VIII.* and *IX.* nerves (fig. 135). Moreover, the *X.* nerve has come inside the auditory capsule, as the capsular wall lateral to the pila occipitalis is incomplete. Thus the *X.* nerve runs dorsal to the posterior basicapsular commissure inside the auditory capsule and issues from it together with the *IX.* nerve.

The mandibular arch is as in the preceding stage, but the details of its connections are more distinct in the 47 mm stage and will therefore be considered here. The palatoquadrate proper is connected by a thin membrane with the lateral mesenchyma of the trabecula (fig. 133), with the polar cartilage and with the basal part of the antotic cartilage (pila antotica). More caudally it is connected with a ventrolateral anterior part of the basiotic lamina. This connection consists of a thick lamina of cells arranged more densely than in the surrounding parts. This part of the lamina is pierced by the efferent pseudobranchial artery, the orbital artery and the palatine nerve. The development of this thick lamina could be traced back to the 21.5 mm stage of development. In this early stage the rudiment of the mandibular arch is connected with a broad lateral mesenchymatic field lying inside the constrictor muscle rudiment in front of the spiracular canal and medially extending to the lateral wall of the most frontal part of the mouth cavity. In this field runs the mandibular artery (pseudobranchial), and the palatinus nerve is embedded in it. In the 36—38 mm stages the corresponding mesenchymatic field is easy to determine. It is, however, enlarged and a lateral part of it has cells more densely arranged than its mid portion. The lateral part is the rudiment of the prespiracular complex, the medial is in process of forming the thick lamella of the 46—47 mm and later stages. In this portion the palatinus nerve is embedded. The mid-portion consists of a not very dense mesenchyma and contains the pseudobranchial artery. The medial rudiment is connected not only with the palatoquadrate but also with that of the opposite side by a mesenchymatic band lying close to the symphysial part of the palatoquadrate immediately ventral to the anterior pouch of the mouth cavity.

The "lateral commissure" and the spiracular cartilage rudiments (fig. 133) are as in the preceding stage, but at the basis of the handle of the club-shaped spiracular cartilage rudiment a lateral mass of cells extending towards the lower and anterior part of the spiracle represents the rudiment of a small

cartilage, over which, in the adult, the tendon of the musculus levator rostri passes in a grove on its outside. This cartilage possibly represents a branchial ray belonging to the mandibular arch. In the present stage a new structure is well distinguishable, viz. an anterior ray-like element extending from the anterior part of the rudiment of the muscular crest of the palatoquadrate and pointing like a flattened rod towards the spiracular cartilage, of which it covers the most anterior part on the outside. Dorsally it is inserted into the auditory capsule (postorbital process). This rod of mesenchyma does not differ morphologically from such other mesenchymatic structures as subsequently turns into cartilage or ligament. Later on the actual structure becomes a ligament. (fig. 133, *lig.*).

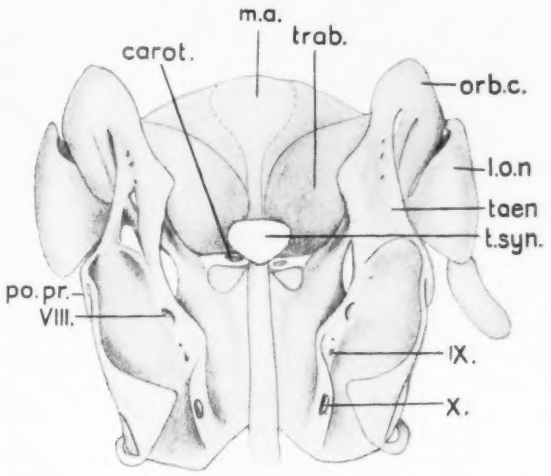

Fig. 135. *Raja.* 47 mm. Skull. Reconstruction. Dorsal aspect.

The tectum synoticum (figs. 133, 135, *t.syn.*) is foreshadowed by an unpaired independent cartilage rudiment in the dorsal midline on a level with the anterior part of the auditory capsule.

Raja clavata, stage 50 mm (56 days after oviposition).

The chondrified external wall of the auditory capsule bends up to the dorsal side of the auditory vesicle. In the 47 and 50 mm stages the taenia marginalis is fused on to the medial side of the obtuse anterior end of the capsule, and the supraorbital crest (figs. 136, 137, *s.cr.*) is connected with the external wall of the capsule and ends with the processus postorbitalis (fig. 136, *pr.po.*). Fusions and chondrifications have taken place in this region. In the 50 mm stage the postorbital process establishes a ridge on the outside of the capsule, separated from it by some fine foramina containing ophthalmicus superficialis and oticus *VII* nerve fibres. The triangular opening between the taenia marginalis and the supraorbital crest has decreased to a foramen (figs. 136, 137, *orb.a.b.*) at the frontal end of the auditory capsule, pierced by a branch of the orbital artery (external carotid) running to the dorsal side of the skull. As in the preceding stage, the vagus nerve runs through the auditory capsule (fig. 139, *b.*). This nerve leaves the capsule through a foramen directed outwards and backwards, situated on the posterior surface of the capsule. This foramen was left open, when the roof formed from the posterior cartilage of

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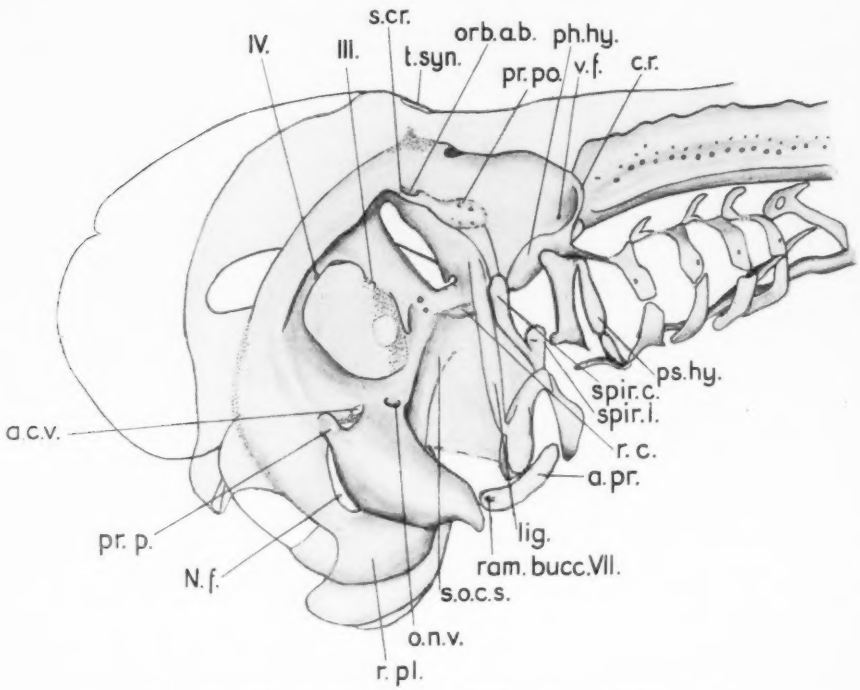

Fig. 136. *Raja*. 50 mm. Skull. Reconstruction. Lateral aspect.

the auditory capsule. The formation of the roof of the posterior part of the capsule was established ventrally to the vena cerebralis posterior accompanying the vagus nerve. Thus this vein does not enter the auditory capsule directly. Instead it is embedded in the roof of the capsule (fig. 137, *p.c.v.*), and as this roof ends anteriorly, the vein bends down in the capsule, ultimately attaining the brain cavity through the inner vagus foramen. This vein, thus behaves differently in *Raja* and in sharks. The bent cartilaginous rod (*c.r.*) in the preceding stage inserted below the glossopharyngeal nerve has chondrified, and its upper tip has joined the auditory capsule dorsal to the jugular vein (v. capitis lateralis), which thus runs together with the nervus glossopharyngeus and vagus through the arch formed by this cartilage (fig. 139 b). The glossopharyngeal nerve is accompanied by a branch of the jugular vein. This branch, however, leaves the auditory capsule through a small special foramen anterior to the glossopharyngeal (fig. 136)) A blood-vessel coming from the brain cavity enters the auditory capsule through a small foramen anterior to the inner glossopharyngeal foramen (fig. 139 a).

The structure described in the preceding stages as the lateral mesenchyma of the trabecula in the (47 and) 50 mm stage has developed into a "subocular shelf" (fig. 136, *s.o.c.s.*), extending from the nasal capsule in front to beyond

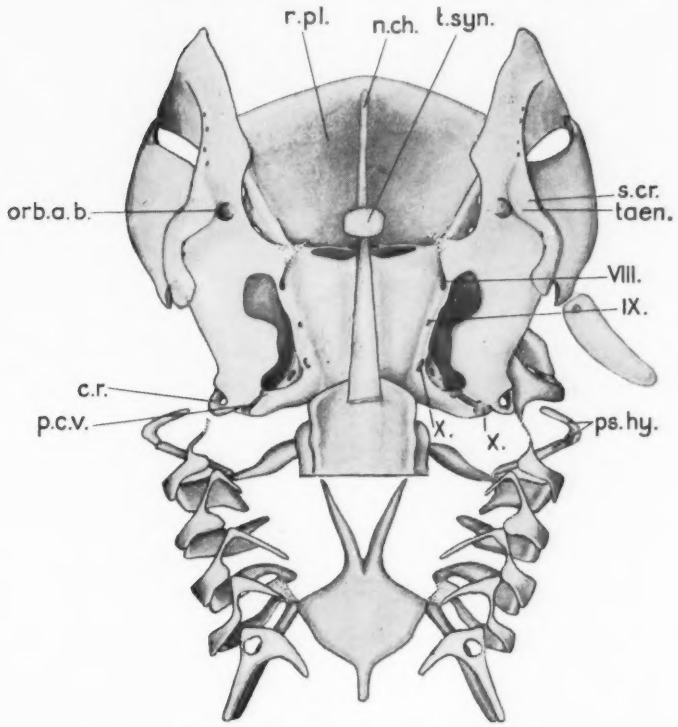

Fig. 137. *Raja.* 50 mm. Skull. Reconstruction. Dorsal aspect.

the orbital artery and the palatinus nerve caudally. The trabecular portion of this shelf is fused with the lateral side of the trabecula and the polar cartilage. This trabecular shelf portion is connected by a very thin membrane with the palatoquadrate. It is continued caudally by a "shelf" connected with the anterior ventrolateral part of the basiotic lamina. Further this shelf is connected with the palatoquadrate. The lower part of this connection is thick, and, as has been shown in the preceding stage, probably belongs to the prespiracular complex. The shelf, except the proximal basiotic portion, is membranous and remains so. It is located perpendicularly to the basis cranii. The proximal basiotic portion chondrifies in connection with the basiotic lamina.

The unpaired cartilaginous rudiment (figs. 136, 137, *t.syn.*) of the cranial roof developed in the 47 mm stage has now grown larger. It consists of a medial, independent, rounded cartilage plate (figs. 136, 137, *t.syn.*), towards which blastematic processes from the anterior part of the otic capsule are directed (fig. 137, 138). The latter are the paired rudiments of a tectum synoticum. It must, however, be mentioned that the unpaired plate and these

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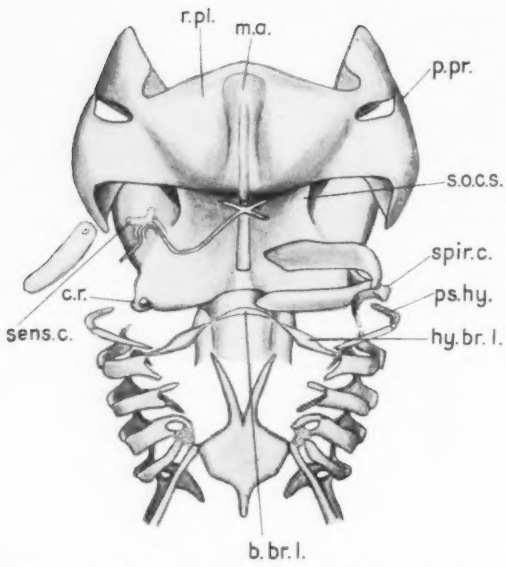

Fig. 138. *Raja*. 50 mm. Skull. Reconstruction. Ventral aspect.

processes lie in a well developed membrane, which completely covers the dorsal side of the brain.

At the lower border of the orbital cartilage the trochlear nerve has become enclosed in a foramen (fig. 136, *IV.*). The orbital cartilage has already in earlier stages, including the 50 mm stage, been connected with the "anterior sideplate" of the trabecula, and also (in the 50 mm stage) with the anterior part of the rostral plate (figs. 136—138, *r.pl.*). Through the development of the anterior connection the anterior border of a vertical fenestra (fig. 136, *N.f.*) has developed. Most of this fenestra lies inside the nasal capsule and contains the olfactory bulb. The medial area is developed as in the preceding stages, but with the difference that the deep part of its frontal end forms a part of the cranial wall in front of the trabecular plate. In the region of the trabecular (rostral?)[1] plate the medial area forms the connection between the two trabeculae forming the main part of this plate. The superficial portion of the medial area forms the big medial keel on the ventral surface of the trabecular (rostral) plate, as in the preceding stages.

The nasal capsule is as it was in the 47 mm stage, but it now has a new cartilaginous connection with the brain-case, viz., with the anterior sideplate between the foramen for the anterior cerebral vein and the orbitonasal vein. The foramen of the latter has been formed through this connection.

Beyond the posterior part of the capsule lies the blastema of the rudiment of the "antorbital" cartilage (*a.pr.*), typical to rays. It is pierced by a branch of the ramus buccalis *VII*. Already in the 40 mm stage, a skeletal rudiment was seen arising from the mesenchymatic envelope of the infraorbital sensory canal. In the present stage this rudiment, corresponding to ALLIS (1919) upper labial cartilage, lies upon the infraorbital sensory canal. The canal behind the olfactory organ has left its position close to the skin and sunk into the tissue on the posterior side of the olfactory organ. On a level with the dorsal border of the nasal aperture the canal returns to the skin before entering

[1] It is no longer possible to make a clear distinction between rostral plate and trabecular plate.

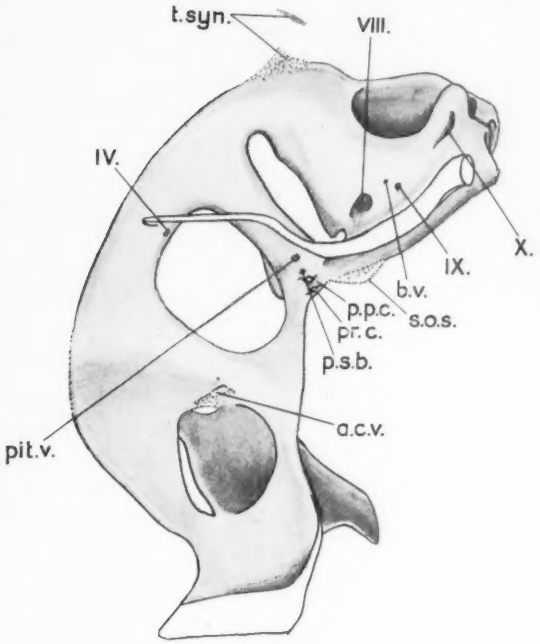

Fig. 139 a.

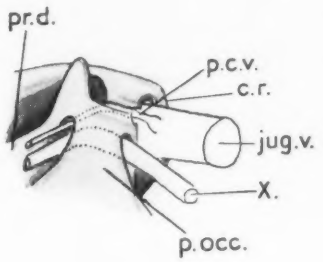

Fig. 139 b.

Fig. 139 a. *Raja.* 50 mm. Skull. Reconstruction. Medial aspect.

Fig. 139 b. *Raja.* 50 mm. Occipital portion. Reconstruction. Medial aspect.

the superficial part of the supraorbital canal. At the dorsal side of the deepest part of this canal the said rudiment is situated as a horseshoe-shaped blastema (fig. 138, *sens.c*). This blastema clearly makes part of the connective tissue mantle of the sensory canal and thus the future cartilage here must be a sensory canal cartilage, and the "upper labial cartilage" of ALLIS cannot therefore be a labial cartilage comparable with other labial cartilages. A rudiment, which is present also in all preceding stages, corresponds to the "ala nasalis" (ALLIS) or annular cartilage (MORI). It belongs to the primary nasal capsule.

In the region of the spiracular canal two blastematic prespiracular rudiments, a dorsal (fig. 136, *spir.c.*) and lateral (fig. 136, *spir.l.*), are present, as in the 47 mm stage. The lateral is situated almost in the angle between the afferent pseudobranchial artery and its branch to the muscles of the mandibula. Other appendages of the palatoquadrate behave as before.

The pseudohyoid is divided into two pieces (figs. 136—138, *ps.hy.*). In the hypobranchial arch of RABINERSON a medial basibranchiale (fig. 138, *b.br.1.*) has chondrified. It is separated from the hypobranchiale I (*hy.br.I.*), which is still connected with the first branchial arch. The dorso-caudal process of the hyomandibula continues caudad as a mesenchymatic strand to the upper end of the pseudohyoid (fig. 136). The pharyngobranchials are now separated from their epibranchials (fig. 136). On the basal part of each

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of the anterior pharyngobranchials a process extends towards the next epibranchial (figs. 136—138). These processes are continued by blastematic strands connecting with the next epibranchial. In the hyoid arch a blastematic strand from the pharyngohyal corresponds as already explained to those strands just mentioned. That rudiment which in the preceding stage lies between the lower end of the hyomandibula and the mandibular articulation, has now fused with the lower end of the hyomandibula, here forming a rounded process. The three anterior ceratobranchials have ventrally a caudal process extending towards the next arch.

Raja clavata, (55-) 58 mm stage (65 days old).

Already in the 55 mm stage the rudiments of the tectum synoticum have reached the medial cartilage plate described in the preceding stage. From the cartilage bridge thus established a taenia medialis extends caudad. This taenia is in the 58 mm stage connected through prochondrium with the inner wall of the auditory capsule (fig. 141) thus no perforation between the brain cavity and the auditory capsule has been left, as in *Squalus*. The kidney-shaped dorsal opening in the auditory capsule of the 50 mm stage (fig. 137) has decreased, leaving as remainders the foramen endolymphaticum (fig. 141, *f.end.*) and the fenestra vestibuli (*f.vest.*), separated by a cartilage bridge extending from the roof of the auditory capsule to that of the braincase (as in *Squalus*). In addition to these two foramina of the roof of the auditory capsule there are present, two other foramina, which are spared as the roof was formed. These two foramina lie in the caudal part of the capsule. The anterior portion of them is pierced by a slender nerve fibre (*X.br.*) belonging to the nervus vagus. The posterior foramen (*v.f.*) opens into the canal of the vena cerebralis posterior. It contains a vein running to the sides of the vertebral column. As Morris (1929) has pointed out, the fossa parietalis is shallower in rays than in sharks. This is due to the fact that the taenia medialis lies on a level with the roof of the auditory capsule in rays and below it in sharks. The internal arrangement of the posterior part of the auditory capsule is simpler than in sharks. As seen from fig. 141, in which the roof of the left capsule has been removed, only a slender cartilage bridge, enters between the lower and the upper parts of the posterior semicircular canal. The anterior part agrees with that in sharks. Through the development of a procartilaginous bridge the posterior branch of the acoustic nerve has become enclosed in a short canal.

The angle between the trabeculae and the parachordals has straightened out considerably (fig. 140) There is no dorsum sellae in *Raja* and no hypophyseal fossa. In *Raja* the postpituitary commissure (fig. 142, *p.p.c.*) forms a strong bridge below the notochord, in its posterior part fusing with the parachordals, whereas the anterior portion is separated from the notochord

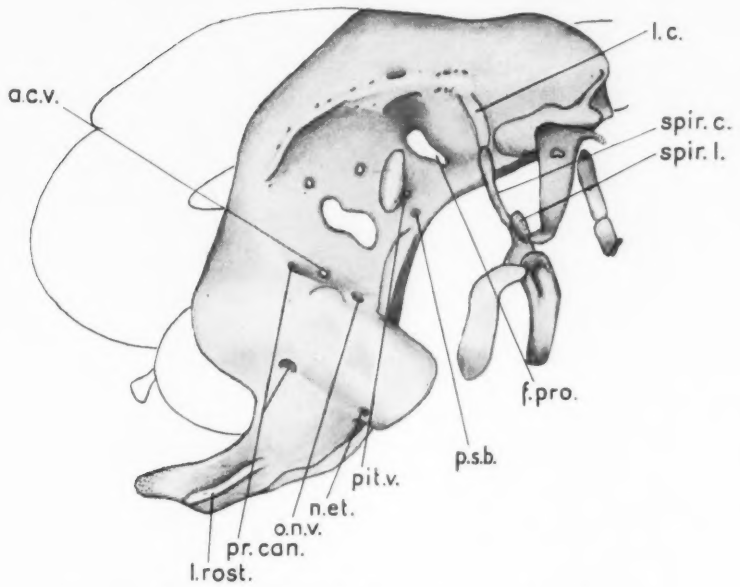

Fig. 140. *Raja*. 58 mm. Skull. Reconstruction. Lateral aspect.

by the acrochordal tissue. The perforation caudal to the commissure (fig. 142) is later on closed by a thick membrane in which a medial part chondrifies together with the postpituitary commissure and by degree closes the perforation. The praecarotid commissure issues from the same lateral part as the postpituitary (fig. 142).

The medial keel (of the trabecular plate) continues frontad as a vigorous rostrum. A blastematic lamella (figs. 140, 141, 142, *l.rost.*) has arisen at its lateral side. Caudally this lamella is connected with a ridge on the anterior part of the trabecular plate. Laterally, the lamella is connected with a superficial blastematic mass connecting the rostrum with the "antorbital process" (fig. 142). The significance of this structure will be discussed later. PARKER has already illustrated the anterior part of the lamella, interpreting it as a labial cartilage.

The upper part of the prootic foramen (fig. 140, *f.pro.*) has, as a result of chondrification in its membranous covering issuing from the taenia marginalis, become closed. This foramen is never divided by any connection between the pila prootica and the auditory capsule. The vena cerebralis anterior (fig. 140, *a.c.v.*) has become enclosed in a foramen. The dorsal border of the lateral nasal cartilage is broadly fused with the lateral side of the orbital cartilage, with the result that the ramus ophthalmicus superficialis *VII* and profundus *V* have been enclosed in the cranial cavity. The nerves return to the surface of the skull through a foramen at the anterior dorsal corner of the nasal

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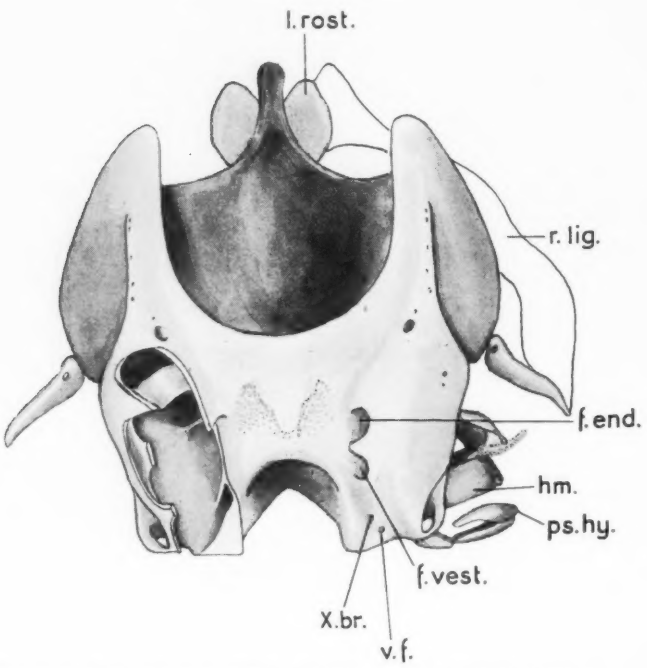

Fig. 141. *Raja*. 58 mm. Skull. Reconstruction. Dorsal aspect.

cartilage (fig. 140, *pr.can.*). During their passage through the cranial cavity the nerves branch off a nerve division (ramus ethmoidalis) (figs. 140, 142, *n.et.*) which runs ventrad and enters the nasal capsule, leaving it again through a foramen at the ventral anterior corner of the capsule. The canal of this nerve is the "ethmoidal canal" of GEGENBAUR. In the 50 mm stage this ethmoidal branch, after separating from the ophthalmicus superficialis + profundus, runs between the lower border of the lateral wall and the lateral border of the medial wall of the nasal capsule. As the space between the two walls subsequently closes up, the nerve becomes enclosed in the capsule. The "ethmoidal canal" in *Raja* thus differs from that of *Squalus* and *Etmopterus*. Lateral and antero-ventral to the posterior opening of the praeorbital canal the orbitonasal lamina is thickened to a ridge or crest, a continuation of the supraorbital crest.

Where the anterior wall of the nasal capsule joins the trabecular plate a caudally directed medial nasal cartilage rudiment (fig. 142) is present. The ala nasalis or annular cartilage like a horseshoe (fig. 142, *a.c.*) surrounds the nasal aperture. Its lateral flap which is somewhat bent mediad chondrifies independently as in *Scyllium*. From the medial part of the rudiment of the sensory line cartilage (fig. 142, *scns.c.*), the socalled nasal-flap cartilage extends into the nasal flap (*n.f.c.*).

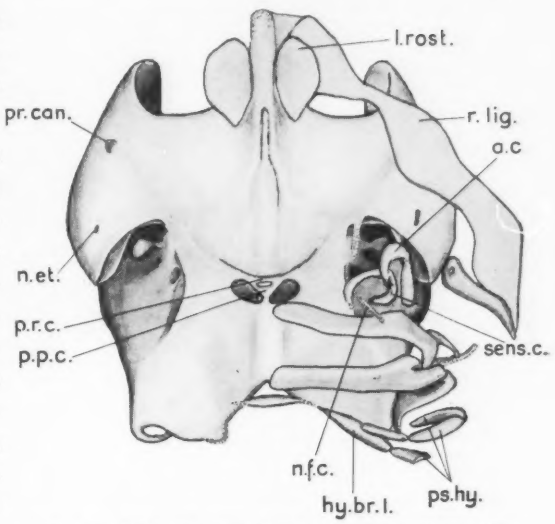

Fig. 142. *Raja.* 58 mm. Skull. Reconstruction. Ventral aspect.

A palatoquadrate- as well as a mandibular symphysis is present. The anterior spiracular cartilage rudiment has chondrified. It articulates against the posterior (lateral) which attains the anterior ventral articular process of the hyomandibula (fig. 140). Other structures belonging to the palatoquadrate complex are as before. On the lateral side of the hyomandibula, a small spherical independent cartilage has developed (fig. 140), in connection with the insertion of the musculus levator hyomandibularis. It is free in the 55 mm stage. In the 58 mm stage it has fused with the hyomandibula. That ligament rudiment, in earlier stages (46 mm and earlier) joining the pharyngohyal with the first epibranchial, in later stages (50 mm) is also joined on to the upper caudal end of the hyomandibula. In the 55 and 58 mm stages the ligament has completely shifted over to the hyomandibula. The pseudohyoid consists of three pieces, of which the inferior contains the ceratohyal. This ventral part of the pseudohyoid articulates against the hypobranchial I (fig. 142).

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Raja clavata, stages 70 (79 days old) and 90 mm.

The external notochordal sheath does not chondrify in *Raja.* The notochord also remains uncovered by cartilage on its dorsal side, and becomes elevated from the parachordal plate, ultimately lying quite dorsal to it in the 90 mm stage.

Already in the 60 mm stage the fenestra hypophyseos is entirely closed, without any foramen for the hypophysial stalk. In the 58 mm stage the anterior part of the prochondrial "wings", (rostral appendix, lateral rostral lamella) (figs. 143—148, *l.rost.*) of the rostrum rudiment has connected up with the anterior part of the rostrum. Laterally they are connected with a dense fascia extending from the rostrum to the antorbital cartilage (figs. 143, 147). In this fascia in the 90 mm stage a small antero-lateral cartilage has arisen (figs. 147, 148), which HOFFMAN (1923) regards as the most anterior part of the pectoral fin skeleton. GARMAN (1913) in the *Synpterygia* (*Rajidae*) describes a "half cartilaginous mass", situated between the anterior border

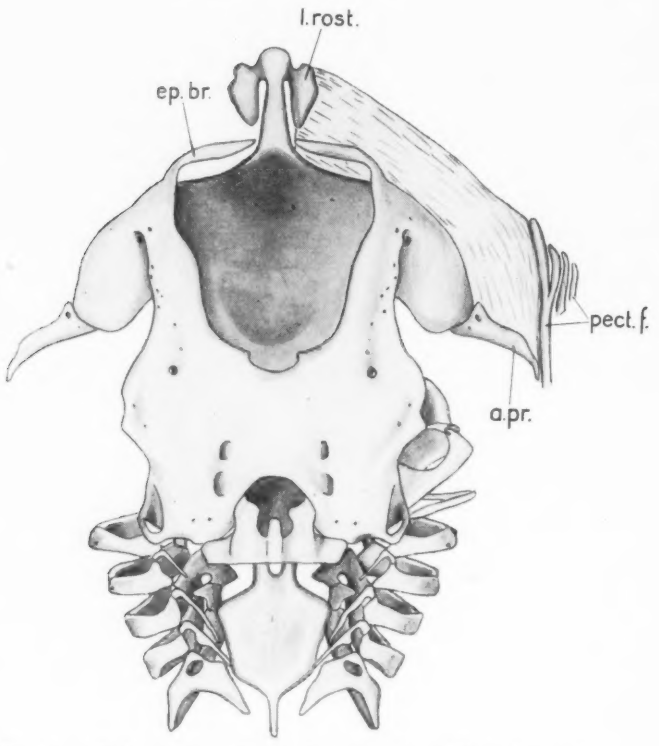

Fig. 143. *Raja.* 70 mm. Skull. Reconstruction. Dorsal aspect.

of the skull, the antorbital process and the pectoral fin. This mass takes the place of the rostrum. It apparently has the same position as the fascia in *Raja,* and could scarcely belong to the fin.

The basal part of the rostrum not only consists of the keel of the trabecular plate but also of the "Schädeldeckenleisten" of MORI. GEGENBAUR found a dorsal concavity of the rostrum in *Rhynchobatus* only. In this genus the prefrontal fontanella extends over a considerable part of the rostrum, and is divided by a cartilage bridge into a posterior and an anterior excavation. The posterior fontanella lies in the posterior part of the orbital region, the anterior in the basal part of the rostrum. A cartilaginous bridge, corresponding to that in *Rhynchobatus,* PARKER (1897) and HOFFMAN (1913) describe as being present also in *Raja,* though it is lacking in GEGENBAUR's figure. In my 70 mm stage this bridge develops as two cartilaginous processes opposite one another and forming in the primary epiphysial bridge blastema (fig. 143—145, *ep.br.*). They are connected with the orbital cartilage. In a 90 mm stage the processes have fused in the dorsal midline of the skull (fig. 147, *ep.br.*). This bridge crosses the epiphysis, the tip of which lies immediately anterior

to it. It corresponds to the epiphysial bridge in the sharks. The anterior fontanella is thus the prefrontal fontanella in sharks. The posterior or frontal fontanella is sometimes closed in rays, always in sharks.

The preorbital crest (figs. 145, 146, *p.orb.cr.*) has become enlarged and forms the anterior border of the orbit. Through the development of the crest, the posterior opening of the preorbital canal has become located at the bottom of a deep posteriorly open pit, anteriorly bordered by the preorbital ridge. The preorbital crest in the 90 mm stage has grown caudally, so that the crest reaches behind the foramen of the anterior cerebral vein. The praeorbital canal has thereby become lengthened with a posterior horizontal part, in which the vena cerebralis anterior has its foramen. The preorbital canal in *Raja* is thus much longer than in the sharks. The preorbital canal in *Squalus* opens in a groove, of which the lateral border is made up of the preorbital cartilage. In *Raja* there is no separate praeorbital cartilage, but a part of the eyebrow area, as already described, forms a process on the dorsal part of the lateral nasal cartilage. In the region of the preorbital canal there is no other wall of the brain cavity than the anterior part of the orbitonasal lamina. The ophthalmicus nerves thus run for a short distance in the cranial cavity. The ramus ethmoidalis runs through the nasal capsule, as in the preceding stage. The orbitonasal canal begins with a dorsoventrally directed foramen in the posterior wall of the nasal capsule. A slender caudally directed cartilage process has developed ventral to the lateral flap of the ala nasalis (fig. 144) in connection with the lower posterior margin of the nasal capsule and lateral to the nasal aperture. In the 90 mm stage this process is separated from the nasal capsule cartilage (fig. 148). A mesenchymatic rudiment was

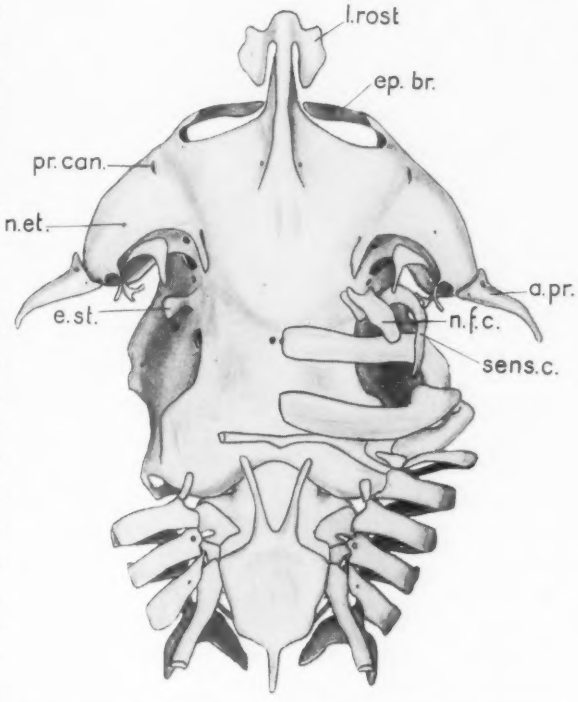

Fig. 144. *Raja*. 70 mm. Skull. Reconstruction. Ventral aspect.

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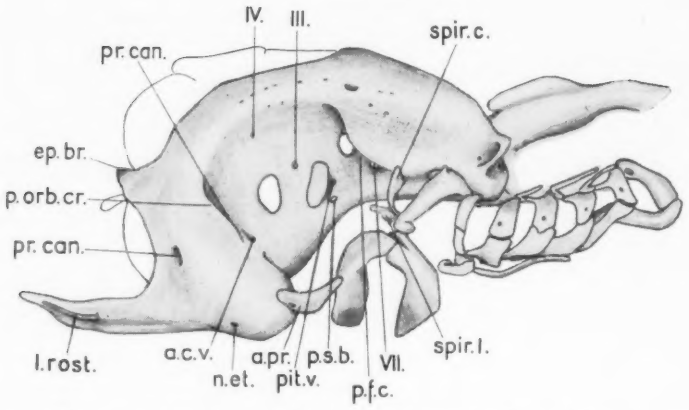

Fig. 145. *Raja*. 70 mm. Skull. Reconstruction. Lateral aspect.

already in the 57 mm stage found lying posteromedial to the nasal opening. This rudiment is chondrified, forming the medial nasal flap cartilage in the 70 mm stage. Already in the 70 mm stage it is a big cartilage plate and has grown considerably until the 90 mm stage (fig. 148, *n.f.c.*). The so-called "labial cartilage" of GEGENBAUR or the sensory line cartilage is also a cartilage of considerable extent (fig. 148, *sens.c.*).

A praefacial commissure (figs. 145, 146, *p.f.c.*) has separated the foramen of the ramus hyomandibularis *VII* from the posterior part of the prootic foramen. This commissure does not chondrify out from the parachordal plate, but from the auditory capsule.

In addition to the medial articulation between the skull and the vertebral column the lateral ridges of the column have attained the medial side of the auditory capsule posteriorly (figs. 144, 145). Caudally the said ridges rise dorsad, causing the formation, on each side of the vertebral column, of a dorsally open groove wherein the spinal ganglia are placed. The roof of the anterior section of the vertebral column developes as two cartilage ribbons lying close to each other and joining the lateral edges of the neural arches. These ribbons in the adult column form the dorsal keel.

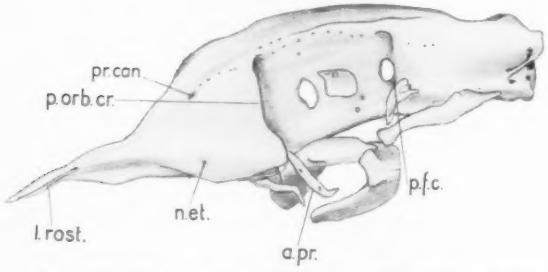

Fig. 146. *Raja*. 90 mm. Skull. Reconstruction. Lateral aspect.

Both praespiracular cartilages (fig. 145) are in contact with the lower articular process of the hyomandibula. The lateral cartilage, consisting in the 70

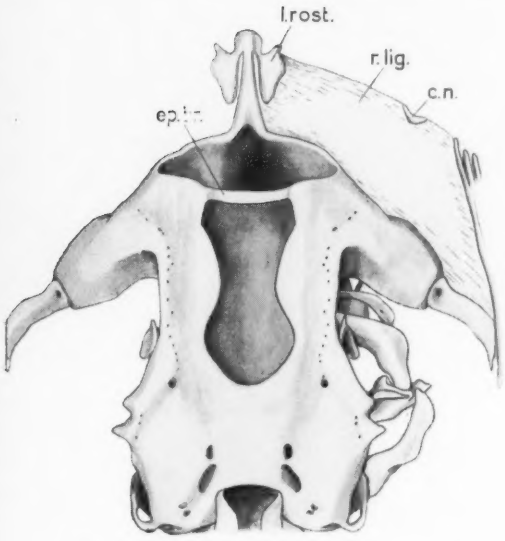

Fig. 147. *Raja.* 90 mm. Skull. Reconstruction. Dorsal aspect.

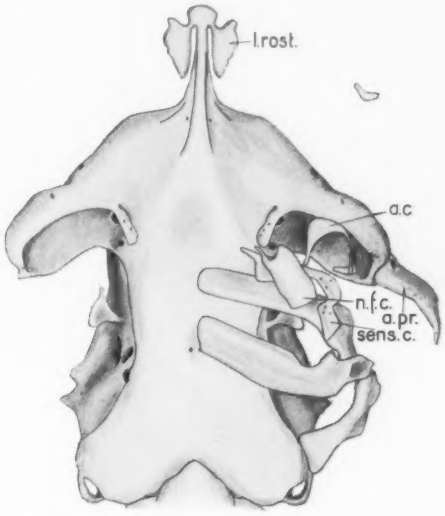

Fig. 148. *Raja.* 90 mm. Skull. Reconstruction. Ventral aspect.

mm stage of prochondrium, and extending frontad medially to the tendon of the m. levator rostri, contains a very distinct cartilage nucleus in the 90 mm stage. The articular disc for the hyomandibula is, as in sharks, undivided and oblong. It is, however, shallower and only on the dorsal side is it bordered by a ridge. The pharyngohyal plate is already in the 70 mm stage completely fused on to the auditory capsule. The pseudohyoid articulates dorsally against the posterior process of the hyomandibula (fig. 145). The lateral blastematic processes of the pharyngobranchials have chondrified and are free from the subsequent epibranchials. The pharyngobranchials are bent at a right angle, seen from above (fig. 143). They articulate against two arches. A similar double connection has been demonstrated by RABINERSON (1925) concerning the hypobranchials. Instead of joining the copular plate the hypobranchials of the third and fourth arches have made contact with the nextfollowing ceratobranchials (fig. 143). On the tip of the second ceratobranchial a small separated part of the second hypobranchial is found.

To this summary description it may be added that the anterior rodlike blastematic process (fig. 136, *lig.*) of the palatoquadrate has become transformed into a ligament connecting the palatoquadrate with the prespiracular muscle in front of the spiracular cartilage. This ligament is connected by another ligament with the postorbital crest.

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TORPEDO[1] OCELLATA.

Torpedo ocellata, stages 15 and 16 mm (with remarks on the 8, 11.5 and 15 mm stages).

The notochord in front is bent quite double with a very short terminal hook portion. In addition, it is somewhat bent down rostrally. The parachordal plates are developed as in *Raja*, being pointed in front. In an 8 mm stage the parachordals are quite blastematic, being clearly outlined and differentiated from the neighbouring mesenchyma. In an 11.5 mm stage they are about to become prochondrial, from behind reaching the level of the anterior part of the auditory capsule. In the 16 mm stage they reach considerably more frontad. They seem to be connected with each other on the ventral side of the notochord, and it is possible that this connection is primary in *Torpedo*.

The acrochordal tissue forms below the anterior end of the notochord a cell bolster (fig. 149, *acr.*), as in other selachians. As in *Squalus* and other selachians, this part of the tissue spreads out lateral wings in the direction of the jugular vein, where they meet a cell mass lying at the medial or medioventral wall of the vein posterior to the pituitary vein. This cell mass contains the primary rudiment of the polar cartilage. In earlier stages, as for instance in the 12 mm stage, it is clearly demonstrated that this rudiment consists of cells derived from that portion of the mandibular somite which connects the rudiment of the obliquus superior muscle with the muscle band of the mandibular arch. In the 15 mm stage these cells are about to separate from the part connecting these muscular rudiments. It is also clear from the 16 mm stage that the cell mass in question also contains the rudiment of the lateral parts of the acrochordal wings, which, like the rest of the acrochordal tissue, are derived from the mandibular somite, as is also the polar cartilage. In the 16 mm stage the rudiment is apparently composed of a dorsal and a ventral portion. The dorsal portion is the rudiment of the antotic cartilage (lateral part of the acrochordal wing) (fig. 149, *a.o.c.*), the ventral that of the polar cartilage (*p.b.*). The separation of the two rudiments does not seem to be complete until chondrification begins in the 18 mm stage, in which the rudiment of the polar cartilage is prochondrial, whereas that of the antotic cartilage is still blastematic. The acrochordal tissue is medially connected (but not fused) with the anterior end of the parachordal (*p.c.*), and the antotic cartilage rudiment which in the 15 mm stage represents the most lateral part of the acrochordal wing is fused caudally with the anterior part of the basiotic lamina, the general development of which has been described (in

[1] As the name "*Torpedo*" is used in all morphological works I have retained it instead of the new generic name "*Narcacion*".

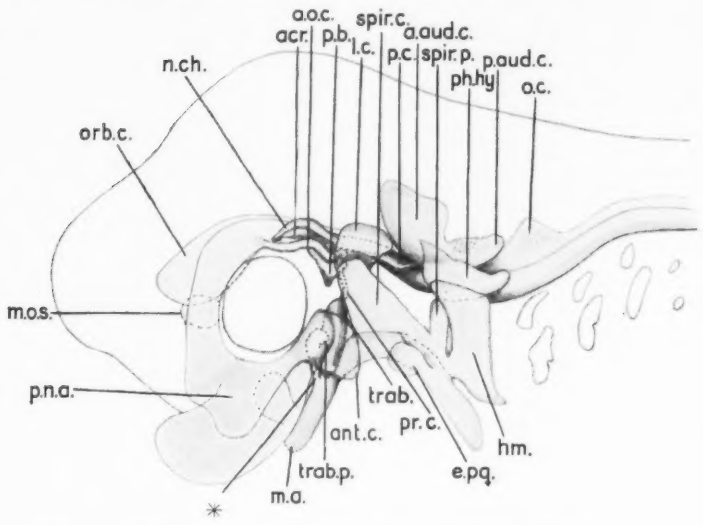

Fig. 149. *Torpedo*. 16 mm. Skull. Reconstruction. Lateral aspect.

Squalus) previously. The anterior end of the antotic cartilage merges without any boundary in the short and diffuse rudiment of the orbital cartilage. The polar cartilage never fuses with the parachordal. The parachordals are already from the very beginning joined to one another below the notochord. They are pointed anteriorly, as in the other selachians investigated. There is a considerable distance between the antotic cartilage and the anterior end of the auditory capsule. Here lies the "preotic lamina", as I shall call the rudiment present in that space.

Between the polar cartilages long and slender postpituitary and precarotid commissures are developed. The latter lies immediately behind the upper (posterior) end of the trabecula (fig. 149, *pr.c.*).

An anterior and a posterior rudiment of the auditory capsule cartilage, relatively independent and still scarcely more than blastematic, are present, as in *Raja* in the mesenchyma surrounding the auditory vesicle in the 15 and 16 mm stage. These two rudiments in the 16 mm stage are not quite independent, but they are connected with each other and with the basiotic lamina with so scanty a blastema that they must have been completely free in a stage but a little earlier than the present one. In the 16 mm stage an anterior and a posterior processus dorsalis arise, forming the rudiment of the medial wall of the otic capsule. They are separated by the glossopharyngeal nerve. This nerve runs dorsal to the posterior basicapsular commissure. Between the two basicapsular commissures is enclosed the wide fenestra basicapsularis. The rudiment of the occipital arch (fig. 149, *o.c.*) is developed as a large triangular blastematic plate behind the posterior medial wall portion. It is

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pierced by one occipital nerve only. The 16 mm stage is interesting as it affords an explanation of the otic shelf portion below the glossopharyngeal nerve. The lateral part of the shelf, which in a 15 mm stage is hardly connected with the basiotic lamina, in the (15 and) 16 mm stage is seen to be the caudal continuation of a large blastematic plate (fig. 149, *ph.hy.*) nearly covering the entire ventrolateral part of the auditory region. Frontally this blastema reaches to the roof of the spiracular canal. Further, it extends caudally as a thick lamella between the efferent hyoid artery (still not joined on to the lateral dorsal aorta) and the vena capitis lateralis (jugular vein). More caudally, it lies ventromedial to the vein and forms posteriorly the thickened border of the "shelf". This large blastema adheres to the ventro-lateral side of the auditory capsule, and is difficult to distinguish from it in the 16 mm stage. In the 15 mm stage, however, where the capsule rudiment is weakly developed, the blastema is separate, forming a unity of its own. From the anterior half of the blastema (in the 16 mm stage) a thin lamella arises, following the lateral wall of the auditory capsule between it and the vena capitis lateralis. The blastematic hyomandibula is inserted into the ventrolateral part of the blastema. In reality the two blastemas are connected with each other by a somewhat less dense blastematic portion. The "shelf" blastema does not belong to the parachordal or auditory skeletal system but to the visceral, and represents the pharyngohyal, as will be more fully explained later on. The shelf portion below the glossopharyngeal nerve is the posterior part of this blastema.

Below the polar cartilages and somewhat distant from them lie the trabeculae (fig. 149, *trab.*). As usual their position is about vertical. In the 16 mm stage each trabecula is spoonlike, with the concavity directed frontad. The two trabeculae do not meet in the midline, since the deep part of the medial area (*m.a.*), as usual, enters between them. Each trabecula has a strong lateral outgrowth (fig. 149, 151, *trab.p.*). The musculus obliquus inferior of the eye bulb is inserted into the dorsal part of its lateral end. This outgrowth apparently corresponds to the lateral jutting-out part of the trabecula of *Squalus* and the lateral blastema in *Raja*. In the 16 mm stage the trabeculae are prochondrial.

A big mesenchymatic mass of cells in the lower eyebrow is connected by means of a short lamella of less densely arranged cells with the lateral end of the trabecular process. These cells represent a part of the future lamina orbitonasalis (*l.o.n.*). This lamella medially bends down below the trabecular process to join (fig. 149*), the medial part of the area. Thus the trabecular process covers the medial part of the lamina orbitonasalis rudiment of this stage. The mesenchymatic cell mass of the eyebrow area contains the rudiment of the rest of the lamina orbitonasalis, including also the rudiment of the "antorbital cartilage" (*ant.c.*) and other structures to be mentioned later.

The large eyebrow mesenchyma narrows down frontally between the eye and the nasal sac, but then widens anterior to an extensive superficial prenasal cell lamella (fig. 149, *p.n.a.*) covering the lateral part of the head in this region. This widened part of the eyebrow area merges dorsally into the upper eyebrow area. Frontoventrally it reaches the lateral border of the deep part of the medial area, which is very broad in the prenasal region.

The orbital cartilage is represented only by a diffuse blastema developing dorsomedial to the eye and anteriorly containing a distinct condensation, in which lies the anterior end of the obliquus superior muscle of the eye (fig. 149, *m.o.s.*).

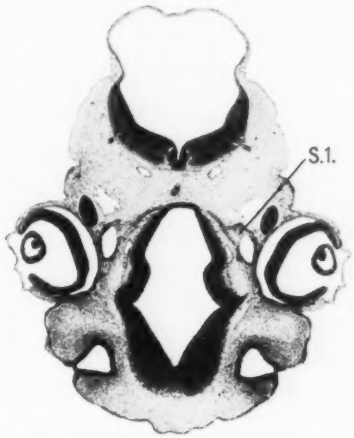

Fig. 150. *Torpedo*. 16 mm. Transverse section of the region of the premandibular somite filling with mesenchyma (eye-stalk).

The mandibular arch of the 16 mm stage is of considerable interest. The palatoquadrate is frontally nearly in contact with the trabecula. It is separated from the trabecula, the polar cartilage and preauditory part of the basis cranii by a large, rather dense and still undifferentiated mesenchyma, which is not clearly demarcated either from the trabecula or from the palatoquadrate. From the dorsolateral border of the palatoquadrate proper rises a big triangular lamella, the upper end of which lies anterior to the auditory organ covering the outside of the jugular vein. This part of the rudiment is a somewhat fibrillar lamella. Ventrally, it is continuous with a big blastema (fig. 149, *spir.c.*) filling the concavity of the muscular lamina anterior to the spiracular canal. It represents a blastema from which the prespiracular cartilage-complex will later differentiate. The ventral part of the triangular blastema is rather thin, decreasing in height caudad, where it enters between the mandibular and the hyoid arches connecting them together. But immediately before this point a blastema rises as a big dorsal process (postspiracular cartilage) (fig. 149, *spir.p.*) to the jugular vein. Caudally, it is loosely connected with the rudiment of the hyomandibula. On the outer surface of the palatoquadrate a big rounded blastema (extrapalatoquadrate) is situated between the epithelium of the oral arch and the posterior part of the palatoquadrate portion of the mandibular arch.

The upper part of the hyoid arch, the pharyngohyal, has already been described as a big blastema joining the auditory capsule. The hyomandibular portion of the arch is inserted into it. This is a somewhat broad blastematic plate not yet differentiated in hyomandibula and ceratohyal. The lower anterior part of its hyomandibular portion is still connected with the mandibular arch

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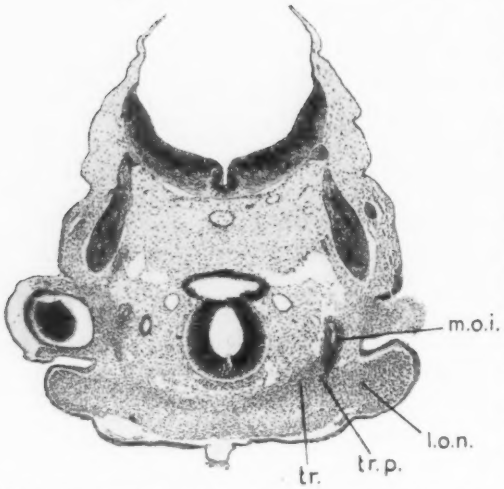

Fig. 151. *Torpedo*. 16 mm. Transverse section of the region of the trabecular process.

and its lower posterior portion sends out a posteromesial process, the future ceratohyal. The pseudohyal is an undifferentiated blastema.

The branchial skeleton is developed as in *Raja*, but the dorsal rudiments do not arise at the point where the efferent branchial arteries bend down but somewhat behind that point. The ventral arch elements reach dorsally to the commissure between the two capillary systems of each branchial arch. Musculus adductor branchialis, primarily passing below and behind the arch, is about to become enclosed in a foramen at its posterior border (fig. 149).

In the 15 mm stage the premandibular somite still has a great open cavity, but its commissure is becoming obliterated in the midline, solid (fig. 150, *s.i.*). In the 16 mm stage the open cavity has decreased owing to a cell proliferation issuing from that part of its wall to which the commissure is attached. At this part a mesenchymatic cell mass (future eye stalk) is filling in the cavity. In addition, the medial wall of the cavity is proliferating cells mediad. These cells form at least part of the rudiment of the orbital wall posterior to the optic nerve. The cavity wall adjacent to the eye is also proliferating cells. These cells join the primary scleral membrane of the eye as in *Raja* and others, causing a distinct thickening of it.

Torpedo ocellata, stage 17 mm.

The notochordal hook is reduced. The parachordals are pointed frontally (fig. 153, *p. c.*), being connected with each other below the notochord. The anterior and posterior rudiments of the auditory cartilages of the preceding stages have fused with each other and with the basicapsular commissures. The anterior commissure is broader than the posterior. The fenestra basicapsularis (fig. 153, *f.bc.*) has diminished so considerably that there is some doubt about its real existence. But there is a place on the ventrolateral side of the capsule, opposite to the lagena and inside the articular head of the hyomandibula, where there is an opening probably representing the basicapsular fenestra. The medial wall of the auditory capsule is somewhat higher than before. The glossopharyngeal nerve enters the auditory capsule through a notch in the

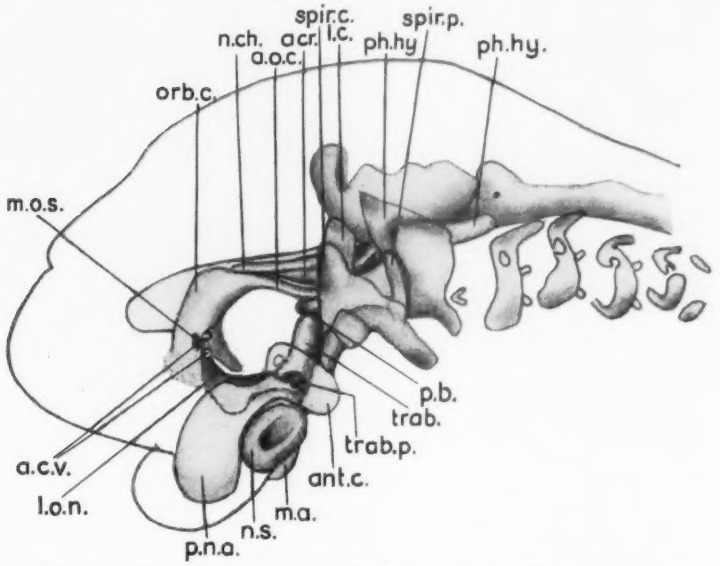

Fig. 152. *Torpedo*. 17 mm. Skull. Reconstruction. Lateral aspect.

medial wall as in the preceding stage. The pharyngohyal blastema (fig. 152, *ph.hy.*) of the preceding stage has fused with the ventrolateral wall of the auditory capsule. The blastema forms "shelf" portions in the anterior and posterior parts. It has been flattened out in its medium part between the hyomandibula and the auditory capsule outside the fenestra basicapsularis, and here it seems to form a sort of articular disc for the hyomandibula. The anterior dorsal lamella between the auditory capsule and the vena capitis lateralis is as in the preceding stage.

The trabeculae have joined on to the polar cartilages (fig. 152), which are fused with the lateral part of the acrochordal tissue. Dorsal to the vena pituitaria the pilae antoticae (antotic cartilage rudiment) are connected with each other by means of the acrochordal tissue. The diffuse rudiment of the orbital cartilages form the frontal continuation of the antotic cartilage (figs. 152, 153, *orb.c.*). The antotic cartilage (*a.o.c.*) rudiment in *Torpedo* seems to be independent only in early stages. The medial area (*m.a.*) frontally

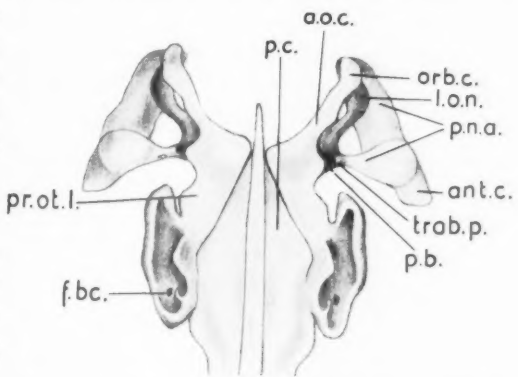

Fig. 153. *Torpedo*. 17 mm. Skull. Reconstruction. Dorsal aspect.

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between the anterior part of the nasal openings is broad. Caudally it becomes narrower. As in the preceding stage, this narrow part enters between the trabeculae, connecting them with each other. Behind and in front of the hypophysial stalk a fusion is about to take place between the trabeculae and the deep part of the medial area. Through this fusion a posterior and an anterior trabecular plate are forming. Of these, the posterior one is augmented as the precarotid commissure fuses with its upper (posterior) margin. The postpituitary commissure has fused with the ventral surface of the acrochordal tissue. As in the preceding stage, the trabecula has frontally a lateral process (fig. 152, 153, *trab.p.*), into which the m. obl. inferior is inserted. The rudiment of the lamina orbitonasalis is fused with the ventral surface of this process. The latter rudiment extends with a thinned part into the bulky mesenchymatic mass of the lower eyebrow area behind the olfactory area. From this thin part and from the eyebrow area a band of mesenchymatic tissue connects with the medial area. That part of the above mentioned eyebrow area which frontally passes between the eye and the olfactory organ narrows down considerably and thins out. Anterior to the olfactory organ it again swells out to a big mesenchymatic mass (fig. 152, *p.n.a.*) forming a prenasal blastema, which is delimited medially by an undifferentiated mesenchyma, which later develops to form the anterior part of the medial area.

From that part of the lamina orbitonasalis which is connected with the lateral process of the trabecula a somewhat bent band of mesenchyma (figs. 152, 153, *l.o.n.*) connects with the frontal portion of the orbital cartilage, thus performing an orbital frame, anterior to the anterior cerebral veins (*a.c.v.*). This band has a frontal broadening near its midpoint. This broadened part lies like a roof over the nasal sac.

The "anterior sideplate" is forming *behind* the cerebral veins (two foramina). It does not yet reach the trabecula. Thus the sideplate develops (in situ) from the dorsal side and later on comes into connection with the trabecula. The premandibular cavity is completely filled in with mesenchymatic cells, representing the eye stalk, which is thus also in *Torpedo* of somitic origin.

The mandibular arch is as in the preceding stage, but the complex of the spiracular cartilage blastema lies more caudally, so that the posterior border of its upper end covers the anterior end of the auditory capsule. The postspiracular blastema is as in the preceding stage. I am not sure that in the connecting bridge between the mandibular and hyoid arches there is not a condensation of the blastema anterior to the efferent pseudobranchial artery, which might represent an independent cartilage rudiment ("Symplectic").

The dorsal rudiments of the branchial arches, growing around the musculi adductores branchiales, have fused with the ventral, whose foramina have already become closed. The pharyngobranchials arise as posterior processes on the dorsal elements, as in *Raja*. In *Torpedo* they have already formed before

the fusion of the dorsal and ventral elements. Rays (fig. 152) develop after the fusion has taken place, one ray dorsal, another ventral to the commissures between the capillary plexuses. Two ray rudiments are also present on the hyomandibula, but they are fused basally. The copular plate is as in *Raja*.

Torpedo ocellata, stage 21 mm.

The notochord rests, as in the preceding stage, upon a parachordal plate. The parachordals, however, do not reach any further frontad than halfway between the auditory capsule and the tip of the notochord (fig. 155). The

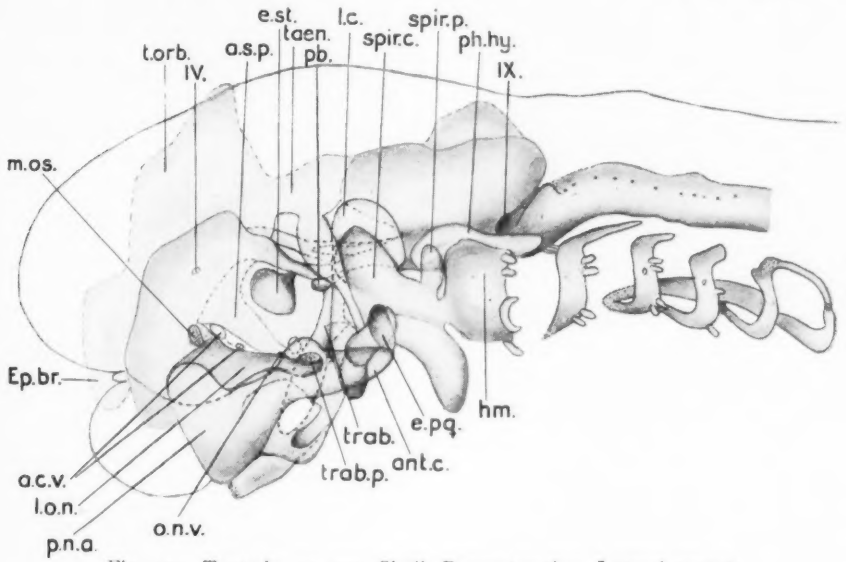

Fig. 154. *Torpedo*. 21 mm. Skull. Reconstruction. Lateral aspect.

auditory capsule in this stage is fully outlined but blastematic. The basicapsular commissures have developed so considerably that the basicapsular fenestra, is reduced, as in the preceding stage, to a small foramen opposite the lagena. The pharyngohyal (fig. 154, *ph.hy.*) has fused with the ventrolateral wall of the auditory capsule forming anteriorly a shelf anterior to the hyomandibular fossa, and posteriorly the external border of the shelf below the glossopharyngeal nerve and ganglion. Its medium part forms a quite blastematic tissue connecting the hyomandibular arch with the auditory capsule. The upper and lower borders of this medium part seem to take part in the formation of the ridgelike borders of the hyomandibular fossa. The anterior dorsal lamella of the pharyngohyal is now degenerating being transformed into undifferentiated connective tissue, which fuses with the auditory capsule. The medial wall of the auditory capsule is a little more developed than before, and the glossopharyngeal notch has become bridged over, so that the glos-

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sopharyngeal nerve (fig. 155, *IX.*) perforates the medial wall. The external foramen for the glossopharyngeal nerve (fig. 154, *IX.*) lies dorsal to the posterior shelf, and is thus invisible from the ventral side.

The pila antotica connects the orbital cartilage which is pierced by the trochlear nerve (fig. 154, *IV.*) with the fronto-lateral part of the acrochordal tissue and with the polar cartilage.

The trabeculae are connected with each other in the medial line by means of the medial area. This connection extends caudally to the carotid artery. The posterior edge of the trabecular plate, however, is bordered by the precarotid commissure fused to it. The lateral process (figs. 154, 155, *trab.p.*) of the trabecula described in the preceding stages seems to have decreased in length. This process is fused laterally with the posterior part of the orbitonasal lamina (*l.o.n.*). The orbitonasal lamina forms an orbital frame frontally (fig. 154), as in the preceding stage. Its broadened anterior part has become prolonged frontad, its ventral border-portion forming a roof over the nasal sac. The orbitonasal lamina lies anterior to the two anterior cerebral veins (*a.c.v.*) as well as to the orbitonasal canal (*o.n.v.*). The posterior part of the lamina orbitonosalis has a medial connection with the medial area by means of a thin blastematic lamella, as already described in the 17 mm stage. This lamella lies immediately below the frontal part of the trabecula. The lower eyebrow area (as in preceding stages) anteriorly forms a large lamella (figs. 154, 155, *p.n.a.*) covering the anterior lateral part of the forebrain outside the dorsofrontal part of the olfactory sac and the fronto-lateral part of the orbitonasal lamina. Caudally, the postnasal part of the eyebrow area extends as a large process (*ant.c.*) into the side border of the body. This process is the rudiment of the so-called "antorbital cartilage" or fin-supporter. Posterior to the anterior cerebral vein lies the "anterior sideplate" as in the preceding stage (fig. 154, *a. s. p.*). Now it has reached the trabecular process ventrally. Membranous rudiments of the epiphysial bridge (fig. 155, *Ep.br.*) and of the tectum orbitale (fig. 154, *t.orb.*) are present. The orbital cartilage is connected with the auditory capsule through a blastematic taenia marginalis (fig. 154, *taen.*). The rudiment of the eyestalk (fig. 154, *c.st.*) is connected with the pila antotica. This rudiment is a large, well-outlined blastema, derived from the premandibular somite, as explained above.

The mandibular arch behaves as in the preceding stage, but a connection has arisen between the anterior part of the palatoquadrate and the taenia marginalis. This connection passes lateral to the lamella connecting the rudiment of the prespiracular cartilage with the palatoquadrate. It is developed together with the musculus levator palatoquadrati and is no doupt a mesenchymatic envelope of this muscle. On the outside of the posterior part of

the palatoquadrate portion of the mandibular arch a long blastematic process (fig. 154, *c.p.q.*) extends towards the lateral surface of the oral arch. This process is bent ventrad. It probably corresponds to the extrapalatoquadrate blastema occuring in other selachians in a corresponding location. A rudiment of the m. levator labii superioris is present on the outside of the palatoquadrate. It is frontally inserted into the posterior margin of the lamina orbitonasalis (fig. 155, *m.lev.lab.*). The rudiment of the prespiracular cartilage is the same as in the preceding stage, and so is also the postspiracular blastema (postspiracular cartilage).

The hyoid arch, of which the pharyngohyal portion has already been described together with the auditory capsule, has acquired (in the 21 mm stage) three new rays, two dorsal and one ventral to the primary two fused rays of the 17 mm stage. The hyomandibula and the ceratohyal together form a broad blastematic plate ventrally curving mediad.

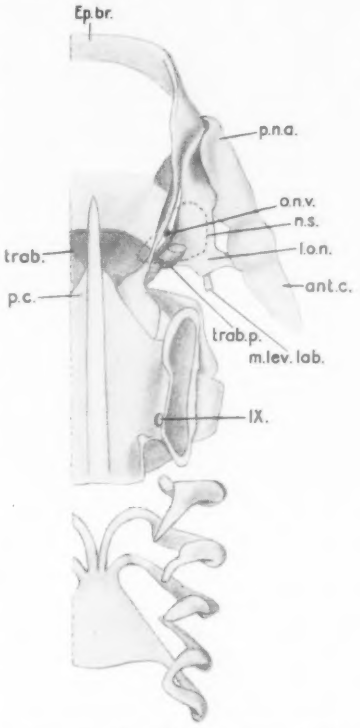

Fig. 155. *Torpedo*. 21 mm. Skull. Reconstruction. Dorsal aspect.

Torpedo ocellata, stage 23 mm.

In the 23 mm stage some important changes have taken place. The hyomandibular nerve, previously passing through a notch in the posterior corner of the prootic fenestra, has become enclosed in a foramen of its own and is separated from the palatine nerve by a procartilaginous bridge. The taenia marginalis is chondrifying anteriorly and posteriorly. The orbital cartilage has grown out considerably. It is broadly connected with the anterior portion of the orbitonasal cartilage, which has broadened considerably and now frontally covers the olfactory bulb laterally, and caudally forms a roof over the olfactory sac. The big mesenchymatic mass of the lower eyebrow area has fronto-ventrally a condensed portion, the rudiment of the rostral appendix of the adult animal. The posterior part of the lower eyebrow area forms the rudiment of the "antorbital cartilage", as in preceding stages. The anterior sideplate is complete, joining the trabecula posterior to the orbitonasal vein. The foramina of the efferent pseudobranchial artery and the pituitary vein are formed, the notches through which they have passed earlier being now closed.

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The mandibular arch, with the rudiments of the prespiracular and postspiracular elements, is as in the preceding stage. The hyomandibular arch has differentiated in the following manner. The big hyomandibulo-ceratohyal plate of the preceding stage has divided into a big dorso-anterior, triangular plate, the hyomandibula, and a postero-ventro-medial smaller portion, the ceratohyal. The hyomandibular branchial rays, now six in number, have joined together basally forming the pseudohyoid, to which the ceratohyal has been added ventrally. The branchial arches each consist of two pieces. At least in the two anterior arches chondrification of the ventral elements has taken place around the insertion of the musculi adductores branchiales, as a result of which "foramina" have again arisen. From the lateral part of the pharyngobranchial portions blastematic processes run out towards the epibranchial portion of the next-following arch.

Torpedo ocellata, stage 24.5 mm.

The straightening of the trabecular angle is not so far advanced as in the figure of *T. marmorata* 24 mm given by DE BEER, in which the angle is about 37°, whereas it is about 60° in the 24.5 mm stage of *T. ocellata*,[1] and also in my 28 mm stage of *T. marmorata*. The auditory capsule has long ago acquired a roof, connecting up at least anteriorly and posteriorly with its medial wall. The acoustic nerve pierces the medial wall. In the region of the ductus endolymphaticus the medial wall has a deep fissure. The fenestra basicapsularis is not yet completely closed.

The auditory capsule now extends caudad as a ridge on the lateral side of the occipital column. In the groove between this ridge and the subglossopharyngeal shelf runs the vagus nerve and opens the foramen for the occipital nerve Z. The occipital nerve Y., with its foramen has disappeared. Vena cerebralis posterior, previously running through the vagus foramen closely to the medial wall of the auditory capsule, is partly enclosed in a canal opening into the vagus canal. The internal arrangement of the auditory capsule corresponds to that of *Raja*. The articulation between the skull and the vertebral column is as in *Raja*, but the medial articulation plug is not so pronounced. The occipital columns pass posteriorly over in lateral, transversely rounded, masses of mesenchym, continuous with the lateral ridges of the vertebral column (fig. 156). These mesenchymatic masses form the rudiment of the lateral condyles of the skull. As they chondrify, the first spinal nerve is enclosed in the cartilage of the condyle.

The junction between the chordal and the prechordal parts of the neural skull is effected dorsally by the broad chondrified taenia marginalis, which closes the incisura prootica to form a foramen prooticum. A supraorbital

[1] DE BEER's representation of a 24 mm *Torpedo ocellata* (1937) tallies better with my results with regard to the trabecular angle.

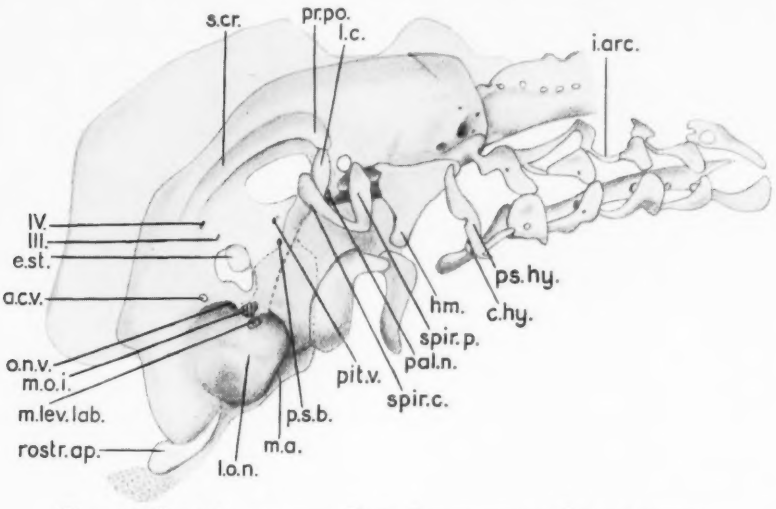

Fig. 156. *Torpedo*. 24.5 mm. Skull. Reconstruction. Lateral aspect.

crest rudiment is present as a blastematic independent border on the orbital plate, extending posteriorly on the frontal part of the auditory capsule, and including a proc. postorbitalis (fig. 156). Ventrally the pila antotica, acrochordal tissue and polar cartilages, forming a unit (fig. 159), have together joined the parachordal plate and the lamina basiotica (fig. 160). The posterior part of the trabecula is also fused with this unity. The pila antotica has broadened considerably, and the pituitary vein as well as the efferent pseudobranchial artery is enclosed in cartilage, produced by chondrification of the mesenchymatic membrane dorsal and anterior to the vessels. The chondrification takes place partly from behind, partly from below. The orbital cartilage has also broadened. The oculomotor nerve thereby has become enclosed. The supraorbital crest rudiment is quite mesenchymatic, and later seems to disappear completely. The connection between the frontal part of the orbital cartilage and the nasal region has broadened very considerably, so that the anterior cerebral (fig. 156, *a.c.v.*) and the orbitonasal veins (*o.n.v.*) have become fairly widely separated from the optic fenestra. Through a broadening of the orbital frame the optic fenestra has thus decreased very much since the preceding stage.

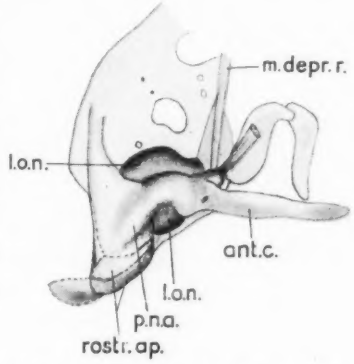

Fig. 157. *Torpedo*. 24.5 mm. Skull, rostral part. Reconstruction. Lateral aspect.

The postpituitary commissure lies immediately below the acrochordal tissue, the lateral parts of which seem to have chon-

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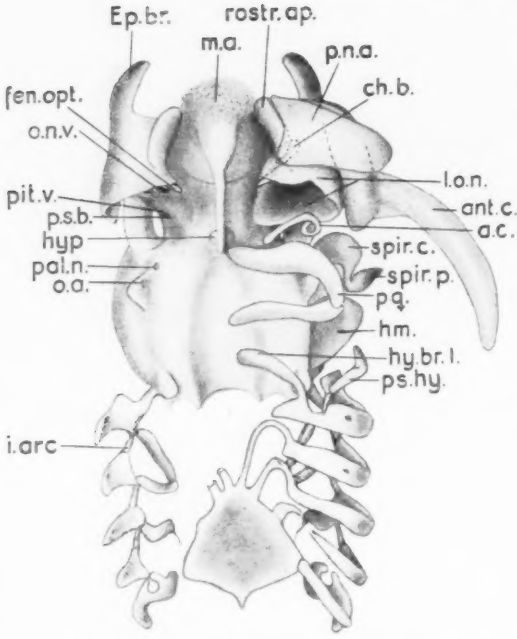

Fig. 158. *Torpedo*. 24.5 mm. Skull. Reconstruction. Ventral aspect.

drified together with the medial basal part of the pila antotica. The precarotid commissure is fused with the trabecular plate in front of the carotid foramen, and in front of that again the foramen for the hypophysial stalk is about to close.

The lamina orbitonasalis (figs. 156—158, *l.o.n.*) below the foramen of the anterior cerebral vein and anterior to the foramen of the orbitonasal vein forms the roof of the nasal capsule and covers the olfactory nerve and bulb in front. The dorsal part of the orbitonasal lamina is thickening through a dense layer, by degrees chondrifying from the primary lamina. It is continuous with the lateral process of the trabecula out of which the m. obliquus inferior (fig. 156, *m.o.i.*) has its origin. In this thickened part of the lamina orbitonasalis the m. levator labii superioris (*m.lcv.lab.*) has its origin lateral to that of the eye muscle. The thickening of the lamina probably has some relation to the strong development of the antorbital process, which requires a substantial support. A ridge in the middle portion of the orbitonasal lamina (fig. 156) serves that purpose. The lamina orbitonasalis is covered on the outside by the lower eyebrow area, which frontally contains the rudiment of the rostral appendix (figs. 156—158, *rostr.ap.*) and caudally extends into the "antorbital process" (*ant.c.*). At the basis of this process there is another short, caudally directed, process, (fig. 157) into which the musculus depressor rostri (*m.dpr.r.*) is inserted. The medium part of the area covers the nasal capsule laterally (fig. 157).

The medial area (fig. 158, *m.a.*) of the 24.5 mm stage is rather indistinctly outlined. It is, however, traceable through its entire length. In the region of the trabeculae it forms a thin medial lamella, of which the deep part has apparently chondrified together with the trabeculae, forming the medial part of the trabecular plate. In the frontal part of the trabecular plate its rostral component is still clearly discernible. In front of the trabeculae the deep portion of the medial area broadens considerably, forming the floor below the

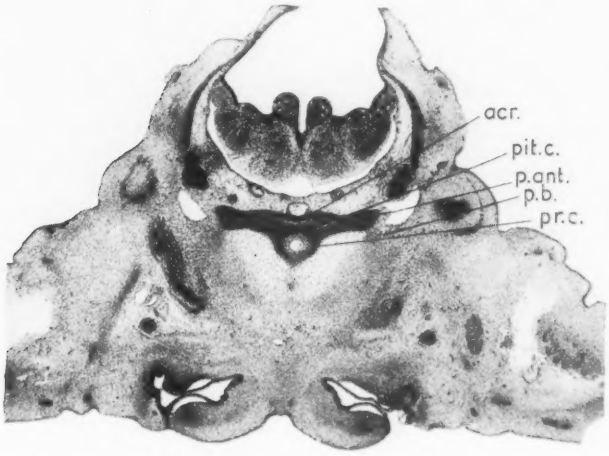

Fig. 159. *Torpedo*. 24.5 mm. Transverse section through the acrochordal region of the head.

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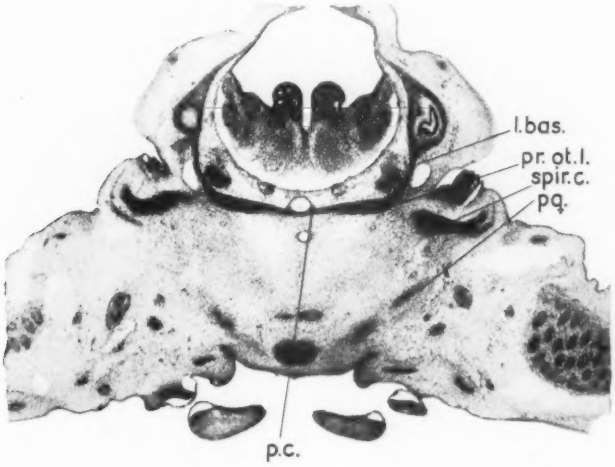

Fig. 160. *Torpedo*. 24.5 mm. Transverse section through the spiracular region of the head.

forebrain. At the rostral end of the nasal capsule this deep portion forms a chondrifying band (fig. 158, *ch.b.*), which extends to the inside of the anterior part of the nasal capsule, forming part of the anterior border of the fenestra nasalis. This band corresponds to the lateral lamellae developing in connection with the "suprarostral process" in *Scyllium*. The broad anterior part of the rostral area between the rostral appendices is quite undifferentiated. This undifferentiated part represents the rostrum of *Squalus* and *Raja*, but in *Torpedo* it does not develop into any cartilage. The annular cartilage (*a.c.*) is developed partly in the nasal flap.

The mandibular arch of this stage consists of the rudiment of the palatoquadrate, the mandibula, and the spiracular cartilages. The palatoquadrate is connected with the neural skull by a mesenchymatic lamella, extending from the upper inner border of the palatoquadrate and attached along a line at the upper margin of the trabecula. The posterior part of this lamella is rather thick, and there the system of spiracular cartilages is inserted into it. A blastematic otical shelf portion (fig. 158) pierced by the orbital artery is present. The prespiracular cartilage (figs. 156, 158, *spir.c.*), which is a broad chondrified plate, behaves as in the preceding stage. The postspiracular cartilage (figs. 156, 158, *spir.p.)* of the preceding stages has developed into a big leaflike blastema, partly connected with the anterior border of the hyomandibula.

The hyomandibula (fig. 156, *hm.*) of this stage is represented by a triangular plate, articulating with its broad basis against the pharyngohyal, which now is completely fused with the skull. Its lower articulation process is not so long as that in DE BEER's figure of *T. marmorata.* It is well separated from the mandibular articulation. Medial to the lower part of the pseudohyoid (figs. 156, 158, *ps.hy.*) lies the insignificant ceratohyal (*c.hy.*). The pseudohyoid is divided into two divisions, together carrying 13 rays. From the basis of the lowest ray a posterior process originates, resting against the outside of the ceratobranchiale I. (fig. 156). In later stages this process becomes more strongly incorporated with the pseudohyoid.

The pharyngobranchials have now become separated from the epibranchials. Their lateral processes reach the next epibranchial, fusing with it as in *Raja.* From the first ceratobranchial a blastema runs out frontad and mediad (figs. 156, 158, *hy.br.I.*). It corresponds to the first hypobranchial of *Raja.* At the lateral border of the copular plate lies the independent rudiment of the fourth hypobranchial, described by FÜRBRINGER (1903). The first epibranchial is connected by a dense mesenchymatic band with the pharyngohyal portion of the skull (fig. 156). For extrabranchials see the 35 mm stage. In the 24.5 mm stage they are prochondrial but developed as in the 35 mm stage.

The 24 mm stage illustrated by DE BEER (1937) cannot be compared in details with any of my stages of *Torpedo,* as the reconstruction demonstrates cartilages only.

A 28 mm stage of *Torpedo marmorata* examined by KÄLLBERG shows such substantial agreement with the 24.5 mm stage of *Torpedo ocellata* that we shall not give any description of it. Comparing KÄLLBERG's figures (not reproduced) with those given by DE BEER of a 24 mm stage of *T. marmorata,* one is struck by the very wide divergences. The DE BEER-stage seems in many respects to have been far more advanced, in others much less advanced

than the 28 mm stage of KÄLLBERG. The figure of DE BEER is incomprehensible in the light of KÄLLBERG's very accurate reconstructions of the chondrified parts of the skull, made with great care.

Torpedo ocellata, stage 31 mm.

KÄLLBERG had selected this stage for the more detailed reconstructions of bloodvessels and nerves, which, however, have already been reproduced in HOLMGREN and STENSIÖ (1936)[1]. The 31 mm stage does not differ very widely from the 24.5 mm stage previously described and therefore some short notes only will be given about the cranial elements.

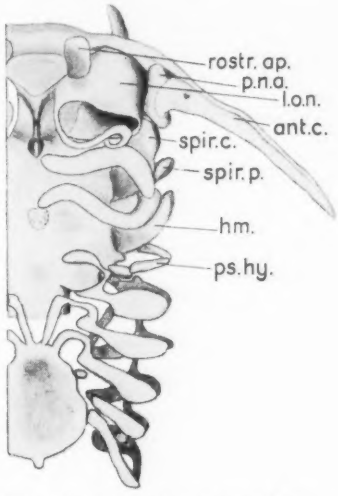

Fig. 161. *Torpedo*. 31 mm. Skull. Reconstruction. Ventral aspect.

The angle between parachordals and trabeculae is about 50—60° (fig. 162). The braincase is covered dorsally with a strong connective tissue membrane (omitted in the fig. 162), forming a complete cranial roof. In the region of the ductus endolymphaticus this membrane is continuous with the medial wall of the auditory capsule. The roof of the auditory capsule is complete except for the fissure in the region of the ductus endolymphaticus mentioned in the preceding stage. The postpituitary commissure has fused with the chondrifying subchordal part of the acrochordal tissue. The two frontal subcerebral branches (*ch.b.* in fig. 158) of the deep portion of the medial area have fused apically with the nasal capsular part of the lamina orbitonasalis anterior to the olfactory tract. In front the deep part of the medial area fills in the space between the two rostral appendices, now chondrifying, and here forms a broad ligamentous band between them (fig. 161), so that this part of the rudiment very closely resembles the rostral part of *Notorhynchus* (*Heptanchus*) *maculatus* (DANIEL). Whether this resemblance is important or only occasional could not be decided as the development of *Notorhynchus* is quite unknown. The superficial part of the medial area of this region has disappeared. In the medial area in front of the palatoquadrate symphysis a distinct rudiment (figs. 161, 162, *m.a.*) is present corresponding to the posterior part of the medial area in *Etmopterus* and *Squalus*, as well as in the *Scyllium* embryo. This rudiment is frontally strongly compressed.

[1] These reconstructions were not quite accurate in regard to the ethmoidal region and the spiracular cartilage complex.

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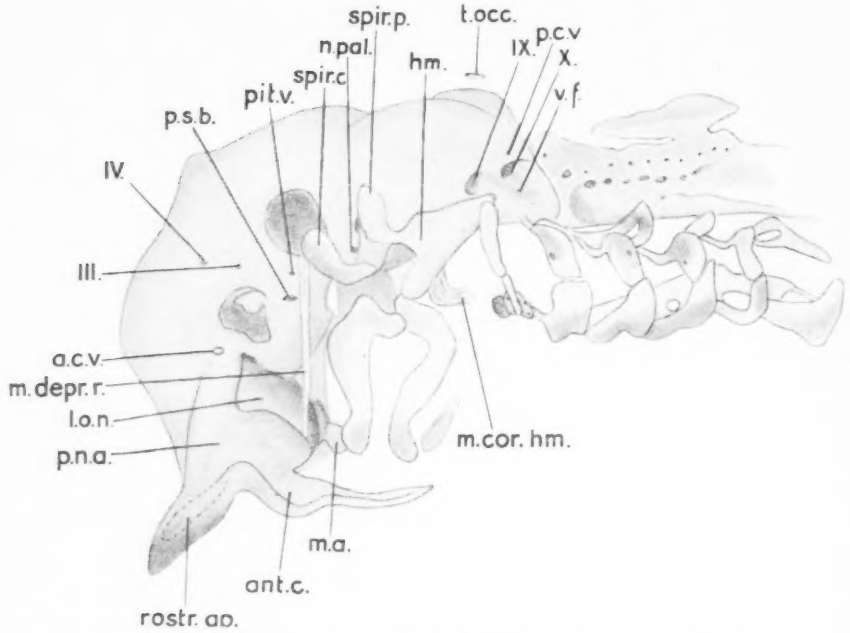

Fig. 162. *Torpedo*. 31 mm. Skull. Reconstruction. Lateral aspect.

Caudally, it widens a little and sends out a ventral process, which enters the medial flap (upper lip) between the nostrils.

The rostral appendices (figs. 161, 162, *rostr.ap.*) are connected, as in the preceding stage, with the eyebrow area and with the rudiment of the "antorbital process" (*ant.c.*). This process is inserted into the nasal capsule (lamina orbitonasalis). Its basal part forms a sort of cushion upon the lateral part of the capsule (fig. 161) and will later chondrify together with the capsule (stage 35 mm), forming two articular processes for the "antorbital cartilage". In the present stage the antorbital cartilage rudiment is still continuous with the cushion, but a separate chondrification is about to begin in the rudiment. A ramification of the buccalis *VII* nerve pierces the rudiment. The rudiment of the antorbital cartilage of the 31 mm stage at its lateral or anterior edge is connected with a rodlike blastema (figs. 161, 162), probably cut off from this edge This rod is the rudiment of the fenestrated bent-down anterior border of the adult antorbital process. Medially, this rodlike rudiment continues into that part of the rudiment of the antorbital lamina which extends against the rostral appendix (figs. 161, 162). The medial end of the independently formed nasal cartilage (annular cartilage) (fig. 161) of the preceding stage has now become connected with a slender skeletal rod, extending from the lower medial corner of the anterior part of the nasal capsule and probably originating from the medial area. The hypophysial

fenestra is closed. A small independent cartilaginous rudiment of the tectum posterius (fig. 162, *t.occ.*) is found in the dorsal medial line of the skull behind the level of the ductus endolymphaticus. The visceral skeleton essentially agrees with the preceding and the following stages. The mandibular arch is connected with the trabecular part of the skull by a strong mesenchymatic mass as in the preceding stage. This mass has now developed into a ligamentous connective tissue, from which two lamellae arise. These lamellae both connect with the medial area. The system of spiracular cartilages is as before, but the connection with the hyomandibula has been more accentuated, as a process has arisen on the anterior side of the latter. The postspiracular cartilage is connected with this process. As this cartilage is also connected ventrally with the prespiracular cartilage the entire spiracular complex has shifted from the mandibular to the hyoid arch. However, it is still also connected with the palatoquadrate. The mesenchymatic otical shelf present in the preceding stage has disappeared. In the hyoid arch an upper and a lower extrahyal rudiment are present. They correspond to upper and lower branchial rays of the pseudohyoid. The first and second pharyngobranchials are connected apically (fig. 162), as in the preceding stage. The interarcual ligaments are chondrifying. The first to the fourth branchial arches have extrabranchials. Each of these have connection with two branchial arches.

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Torpedo ocellata, stage 35 mm.

The floor of the auditory capsule is complete, and its roof is almost entirely fused with its medial wall, leaving only a foramen for the endolymphatic duct. Behind the foramen endolymphaticum the medial wall rises and extends mediad connecting with the rudiment of the tectum posterius already formed in the 31 mm stage. The tectum posterius is the first part of the roof to chondrify. A fenestra vestibuli has become separated from the posterior part of the foramen endolymphaticum. As in *Raja*, the posterior semicircular canal is not visible through this fenestra. In *Raja*, however, the canal lies close to the fenestra, in *Torpedo* it is widely separated from it. In *Torpedo* it is pierced by a strong vein from the labyrinth organ. In the posterior part of the auditory capsule cartilaginous bridges have arisen, separating the semicircular canals as in sharks. A lamella separates the posterior canal from the lagena and connects with the medial wall between the canal and the n. glossopharyngeus at the anterior border of the inner glossopharyngeal foramen. The rest of the posterior canal lies in the glossopharyngeal canal and is thus covered by cartilage chiefly on the dorsal side, as in *Scyllium*. Somewhat dorsal to the external glossopharyngeal foramen there is a small foramen pierced by a small vein (fig. 163). In the mesenchyma connecting the occipital column with the lateral ridge of the spinal column, the lateral cranio-

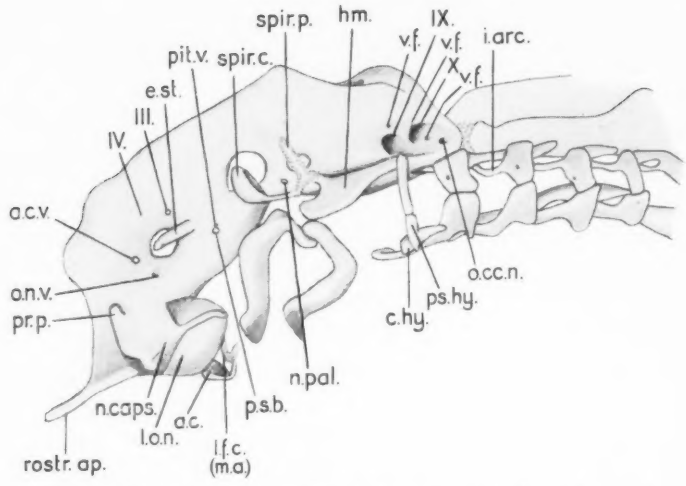

Fig. 163. *Torpedo*. 35 mm. Skull. Reconstruction. Lateral aspect.

vertebral articulation has differentiated (fig. 163). The lateral ridges extend anteriorly as free processes, facing the articular heads of the occipital columns.

The cranial basis is not yet straight (fig. 163). The hypophysial foramen has already disappeared in the 31 mm stage. The eye stalk (*e.st.*) has completely fused with the cranial capsule.

The rudiments of the rostral appendages (figs. 163, 164, *rostr.ap*) have now grown considerably. (In their origin they correspond to the small lateral cartilage processes on the rostrum of *Raja*, but not to the lateral rods of *Scyllium*.) A real rostrum is lacking in *Torpedo* but is ontogenetically represented by the medial area, of which the commissure between the "rostral processes", and the posterior labial flap cartilage (fig. 164, *m.a.*) are remnant structures. The latter corresponds to the "Träger der Nasenflügelknorpel" of J. O. MÜLLER (in *Myliobatus*) and of FÜRBRINGER (1903).

A prochondrial lamella, present as a rod in the 31 mm stage, and perforated by numerous foramina, is imperfectly connected (fig. 164) with the lower side of the anterior border of the antorbital cartilage. The extension of this lamella is demonstrated in the figure 164. In the 24.5 and the 31 mm stage the basis of the antorbital cartilage is connected with the nasal capsule, forming a cushion on the lateral surface of the capsule. This now partly chondrified cushion has separated from the rest of the process, and the antorbital cartilage has been articulated against this cushion of which a medial part has chondrified together with the nasal capsule (fig. 164). The lateral part of the cushion has been transformed into a connective tissue forming an articular disc between the nasal capsule and the antorbital cartilage. The dorsofrontal part of the antorbital process blastema now forms a car-

tilaginous ridge and process below and in front of the eye. It is partly developed upon the primary ridge present already in the 34.5 mm stage. Between the said process (figs. 163, 164, *pr.p.*) and the cranial wall runs the ramus ophthalmicus profundus. This process originating in the eyebrow area, has thus a relation to this nerve corresponding to a praeorbital process. However, it never connects dorsally with the orbital cartilage. The ridge of which the praeorbital process is the upper end is directed frontad, and the frontal part of the antorbital cartilage has acquired a strong support in this ridge (fig. 164).

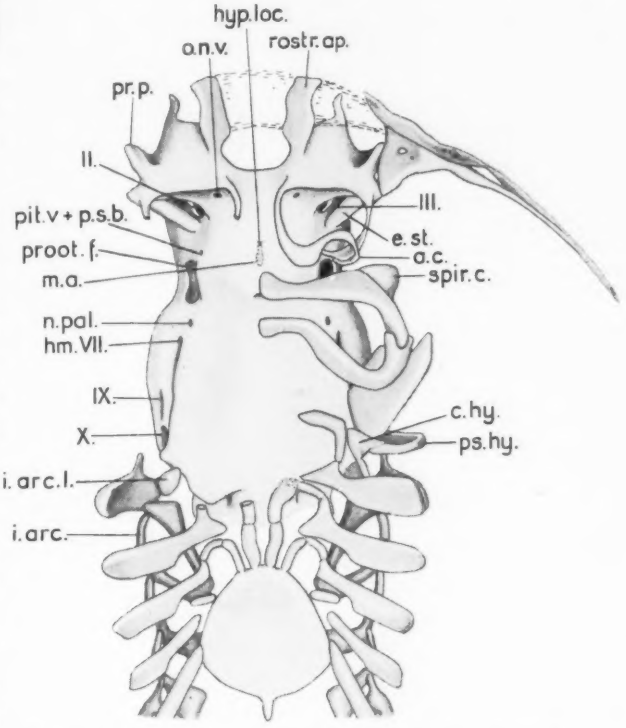

Fig. 164. *Torpedo.* 35 mm. Skull. Reconstruction. Ventral aspect.

In the 28 mm stage of *Torpedo marmorata* a rudiment of a medial nasal cartilage is present as a blastema lying at the medial posterior end of the anterior nasal cartilage. In the 31 mm stage of *T. ocellata* this rudiment is fused partly with the mediocaudal corner of the nasal capsule and partly with the medial end of the rudiment of the annular cartilage. In the rudiment of the lateral wall of the nasal capsule a caudally directed slender band has chondrified (fig. 163, 164). The rest of the lateral wall is membranous (fig. 163). Posteriorly to the nasal aperture this band bends up on the dorsal side of the nasal sac, ending here and broadening to a lamella. Thus the secondary nasal capsule chondrifies only partly.

The hyomandibula has now almost acquired the configuration as DE BEER illustrates it in his 24 mm stage of *T. marmorata.*

The posterior spiracular cartilage (fig. 163, *spir.p.*) has fused with the anterior edge of the hyomandibula. It has grown considerably in a dorsofrontal direction. Medial to the musculus constrictor branchialis, its mesenchymatic connection, with the pre-spiracular cartilage proper, present in earlier stages, has become prochondrial. Its connection with the cartilage lateral

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to the said muscle, which was also originally present, has been transformed into a ligament.

The ceratohyal (*c.hy.*) has fused with the ventral part of the pseudohyoid (figs. 163, 164). Its line of fusion, however, is still visible in the cartilage.

The ceratobranchial rays of the branchial arches have fused with the arch. Those of the epibranchials, on the contrary, remain articulated against the epibranchials. The lowest ceratobranchial ray, the rudiment of the ventral extrabranchial, is not fused with its principal element, and, like the corresponding ray of the pseudohyoid, has a basal process extending medio-ventrally towards the following arch. The ligament connecting each pharyngobranchial with the next epibranchial has chondrified (*i.arc.*) thus strengthening the dorsal part of the branchial basket. On the dorsal margin of each epibranchial the most dorsal ray has developed into a dorsal extrabranchial. Lower extrabranchials are also present. The upper extrabranchials are peculiar as each extrabranchial is connected with two branchial arches. The extrabranchial proper lies in its own arch but from near its middle a band of cartilage connects it with the epibranchial of the next arch immediately in front of the next extrabranchial. The branchial vein passes in front of the extrabranchial proper between it and the extra connection of the next preceding extrabranchial. The first and second pharyngobranchials, as in the 24.5 and 31 mm stages, are fused apically. All pharyngobranchials rest against the vertebral cord. The connecting bridge between the subglossopharyngeal shelf and the first epibranchial has chondrified to a separate cartilage, which, according to WOSKIBOJNIKOFF, is a pharyngohyal, but which in our view is an interarcual (fig. 164, *i.arc.I.*) between the pharyngohyal and the first epibranchial. The ceratobranchial foramina have disappeared. The hypobranchial elements have chondrified and through articulations become separated from the copular plate and from the ceratobranchials. The first and fourth hypobranchial consist of but one piece, the second has been divided into three, the third into two divisions. The two lateral hypobranchial pieces of the second arch are separated by a blastema.

Torpedo ocellata, stages 63 and 71 mm.

The notochord is almost entirely reduced already in the 63 mm stage, and its groove on the dorsal side of the parachordal plate has disappeared. In the vertebral column, however, remnants are present in the vertebral cartilage.

The cartilaginous roof of the skull in *Torpedo* is formed from behind frontad.[1] An anteriorly directed taenia medialis has developed (fig. 165) on the tectum posterius already formed in the preceding stages. In the 71 mm stage it has fused with the now formed tectum synoticum (fig. 168).

[1] All parts of the cartilaginous roof are formed by chondrification of parts of the membranous roof already present in much earlier stages of development.

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In the 63 mm stage this tectum is represented by two opposite processes (fig. 165, *t. syn*) of the anterior part of the auditory capsule. In a 49 mm embryo the processes have already met in the medial line anterior to the taenia medialis. Thus some individual differences might occur in the formation of the cranial roof. No orbital tectum or chondrified epiphysial bridge occurs. As the taenia medialis lies lower than the roof of the auditory capsule a parietal groove is formed, anteriorly bordered by the tectum synoticum (figs. 165, 168). On each side of the taenia medialis portion of the roof, there is present in the roof a pair of rounded perforations (fig. 165), which are later closed by the medial wall of the auditory capsule extending towards the taenia medialis. The incisure in the upper border of the inner wall of the auditory capsule is still present in the 63 mm stage; in the 71 mm, however, it is closed. The cartilage bridge between the foramen endolymphaticum and the fenestra vestibuli stands perpendicular to the cranial surface (fig. 165), as the roof of the auditory capsule lies on a higher plane than the bottom of the parietal fossa. The articular fossa for the hyomandibula is now formed. As the dorsal ridge delimiting the fossa consists dorsally of two separated parts, the fossa in *Torpedo* also consists of two parts, the one anterior immediately behind the foramen for the hyomandibular nerve and the other posterior, in the 63 mm stage ending anterior to the glossopharyngeal foramen, but in the 71 mm stage running out along the large shelf below the vagus nerve. In *Raja* the articular fossa is not divided.

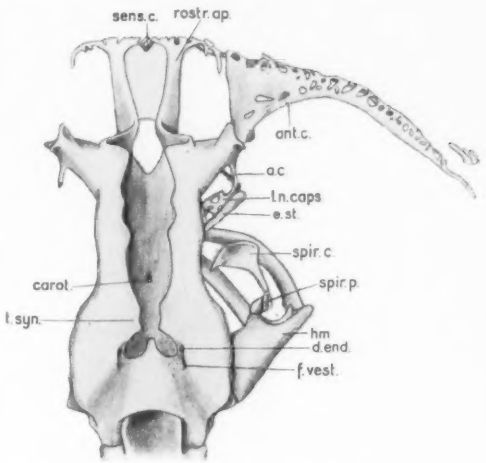

Fig. 165. *Torpedo*. 63 mm. Skull. Reconstruction. Dorsal aspect.

The trabecular angle in the 63 mm stage has almost disappeared (fig. 167). This straightening of the basis cranii has caused some modifications in the relative position of the anterior parts of the skull, which are most conveniently understood if one compares the figures of the 35 mm stage with that of the 63 mm. The rostral processes (*rostr.ap.*) have now grown into strong rods, which articulate against the anterior inner edge of the nasal capsule. Their anterior end is flattened and bent downwards. It is pierced by a number of fenestrations. In the midline between the anterior ends of the processes lies a V-shaped cartilage (figs. 165, 166, 168, *sens.c.*), formed in the mantle of the sensory canal in this part of the head.

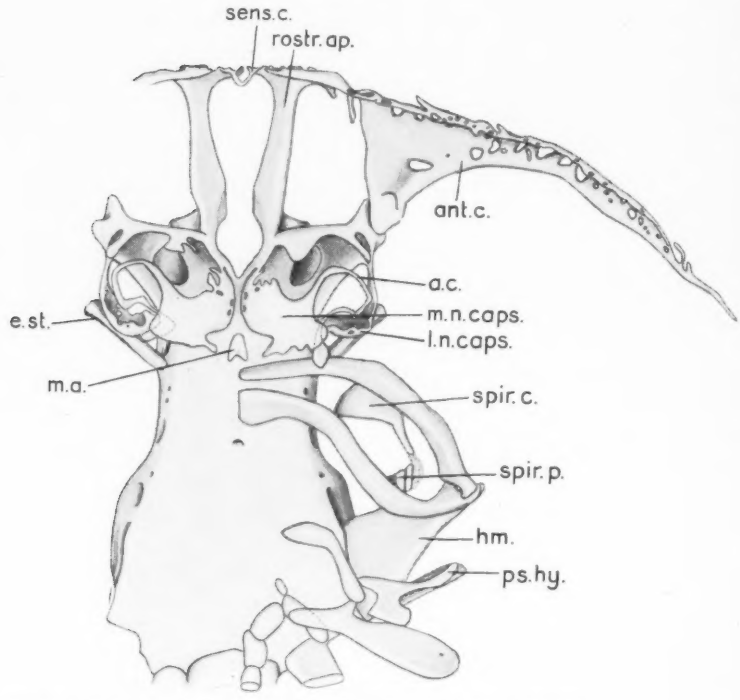

Fig. 166. *Torpedo*. 63 mm. Skull. Reconstruction. Ventral aspect.

The antorbital cartilages (*ant.c.*) have grown into very great structures. They are pierced by a large number of fenestrations. Their articulation against the nasal capsule has been directed frontad, as seen if one compares the 35 mm stage with the 63 and 71 mm.

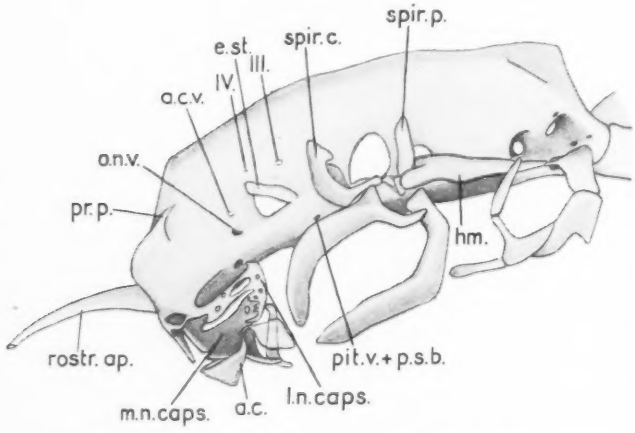

Fig. 167. *Torpedo*. 63 mm. Skull. Reconstruction. Lateral aspect.

The annular cartilage (figs. 165—167, *a.c.*), fused with the medial nasal cartilage (figs. 166, 167, *m.n.caps.*), has ventromedially developed into a great lamella forming the posteromedial wall of the nasal capsule, posteriorly running out with several processes in the nasal flap. From the anterior wall of

the capsule lamellae extend towards the lamella of the annular cartilage. Already in the 71 mm stage some of the lamellae have fused with it. The posterior saucer-shaped part of the lateral nasal cartilage (figs. 165—168, *l.n.caps.*) dorsal to the nasal sac extends also caudad and connects with the ventromedial lamella. In connection with the lateral part of the annular cartilage two vertical lamellae have developed supporting two nasal flaps formed in this region.

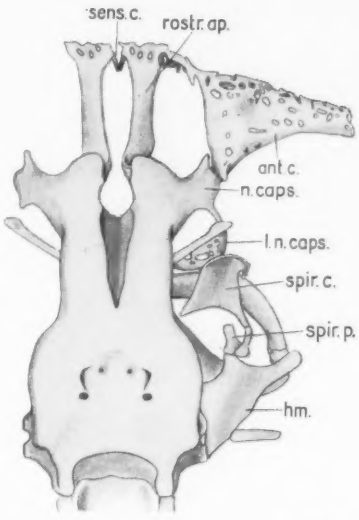

Fig. 168. *Torpedo*. 71 mm. Skull. Reconstruction. Dorsal aspect.

In the posterior part of the palatoquadrate a rudimentary process (fig. 167) is present on its dorsal edge near the articulation head. It reaches to the level of the prespiracular cartilage. No other process is present on the palatoquadrate. The prespiracular cartilage forms a bowlshaped capsule (figs. 165, 167, 168, *spir.c.*) for the pseudobranch and, as in preceding stages, is connected with the posterior spiracular cartilage (*spir.p.*), which is connected with the hyomandibula. It has chondrified. Its ventral end has been severed from its upper part, and is separated from the anterior process of the hyomandibula. Only the ventral end of the upper part is connected with the hyomandibula. The anterior and posterior spiracular cartilages are still connected with each other ventrally. In the 63 mm stage a small cartilage (figs. 165—167) has developed in the connecting part. In the 71 mm stage a new cartilage has developed anteriorly to the former (fig. 168). The cartilaginous chain, in the adult *Torpedo* connecting the prespiracular cartilage with the hyomandibula, has thereby become established. The postspiracular cartilage forms the hooklike process of the hyomandibula in *Torpedo*.

The process running out from the lower part of the pseudohyoid (fig. 166, *ps.hy.*) towards the first branchial arch has become enlarged into a lamella. The blastema formerly connecting the lateral pieces of the second hypobranchial has given rise to a small rounded cartilage (fig. 166), lying anterior to the hypobranchial proper. FÜRBRINGER (1931) considered this cartilage to be an hypobranchiale I and RABINERSON (1925) thought that it corresponds to the anterior tip of that part of the hypobranchiale II which is said to be fused with the copular plate in *Raja*. Its development, however, shows that it is of the same morphological value as the other pieces of the hypobranchiale II in *Torpedo*.

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UROLOPHUS (UROBATIS) HALLERI.

Urolophus Halleri, stage about 27 mm.

The notochord (figs. 169, 173, *n.ch.*) is relatively thicker in *Urolophus* than in *Raja* and *Torpedo*. The parachordals are fused below the notochord (fig. 173, *pc.*), thus forming a single unpaired, anteriorly pointed, parachordal plate (figs. 169, *p.c.*, 171), in the dorsal surface of which the notochord rests in a deep groove. The parachordal plate, anterior to the medium part of the auditory capsule, is well separated from the lamina basiotica (fig. 169). At the anterior end of this parachordal plate the notochord bends dorsad (fig. 173) and ends about on a level with the frontal border of the rostral plate. The preparachordal part of the notochord is thus very long. The tip of the notochord is curiously formed as it is bent double, the caudally directed tip (80 μ long) being a narrow thread lying tightly pressed against the lower surface of the notochord proper.[1] The preparachordal part of the notochord rests upon an acrochordal tissue lamella (figs. 169, 173, *acr.*), narrow and thin at the tip, but broadening and thickening caudally. This acrochordal lamella suddenly broadens immediately in front of the parachordal plate forming the acrochordal wings (fig. 169), which extend towards the antotic cartilages.

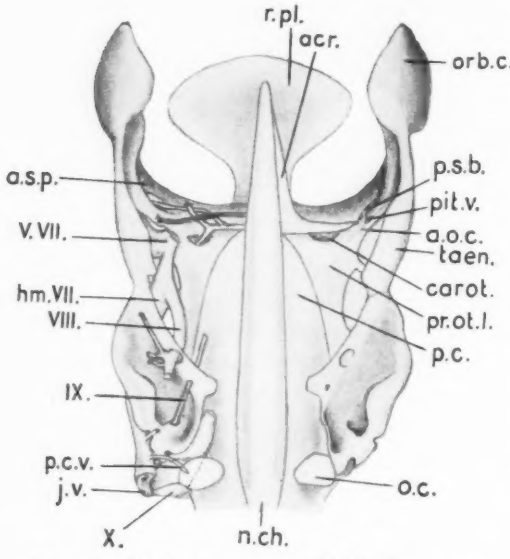

Fig. 169. *Urolophus*. 27 mm. Skull. Reconstruction. Dorsal aspect.

The lamina basiotica is extended along the lateral border of the parachordal. This lamina consists of a preotical portion (figs. 169, 170, *pr.ot.l.*), broad in front, narrower caudally. The 27 mm stage, being too old, did not permit of any analysis of this portion. Its anterolateral corner passes over to the orbital cartilage without any limit. The trabecular complex is connected with the anterior border of the preotic portion of the lamina basiotica. The otical portion of the lamina basiotica forms the floor of the auditory capsule, the inner wall of which seems to be built up of a lamella confluent with the medial border of the basiotic lamina.

[1] This condition signifies an early degeneration of the tip of the notochord.

The blastematic auditory capsule has already been described in outline. Chondrification, however, has begun in its ventrolateral and medial parts. The ventrolateral centres of chondrification in the present stage form a single prochondrial lamella. The following description refers to the chondrifying parts.

The floor of the auditory capsule is already complete (fig. 169). If there has previously been a basicapsular fenestra between the anterior and posterior parts of the basiotic lamina, it is now closed. The glossopharyngeal nerve runs along the floor of the capsule. Apparently there were present originally an anterior and a posterior auditory cartilage, and an incisure at the dorsal border of the auditory lamella indicates that so was the case. Frontally, the anterior cartilage is low, caudally it gradually becomes higher, finally reaching the level of the lateral semicircular canal. The posterior auditory cartilage (behind the incisure) forms a ridge between the sacculus and the external glossopharyngeal foramen. Below this foramen on the outside of the auditory capsule, a small blastematic pedicle (fig. 170, 171, *ped.*) is found. Into the tip of this process is inserted a ligament connected posteriorly with the epibranchial of the first branchial arch.

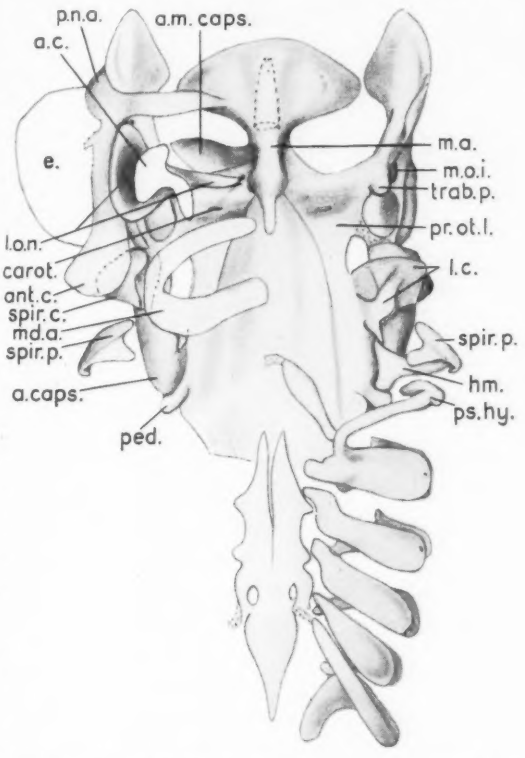

Fig. 170. *Urolophus*. 27 mm. Skull. Reconstruction. Ventral aspect.

The chondrifying medial wall of the auditory capsule (fig. 173) is pierced by the auditory (*VIII.*) and the glossopharyngeal (*IX.*) nerves. Rostrally, it is connected with the orbital cartilage by the strong taenia marginalis (figs. 171, 173). The inner wall of the auditory capsule is highest in the region of the ductus endolymphaticus (fig. 173), where it rises between the duct and the brain. A tectum synoticum, still mesenchymatic, forms a dorsal continuation of the inner wall. Caudally to this part the medial wall is rather low, posteriorly it is fused with the basal part of the occipital column (figs. 169, 171, 173, *o.c.*).

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The dorsal part of the occipital column is bent frontad, forming the dorsal border of the vagus canal (fig. 171, *X.*). Immediately behind the posterior semicircular canal the inner and outher walls of the capsule are fused with a thick cartilaginous part lying below the vagus nerve and forming the floor of the vagus canal. The anterior (lateral) border of the vagus canal is formed by the posterior auditory cartilage, which here reaches the upper part of the occipital column. In the fissure between the upper part of the posterior auditory cartilage and the occipital column runs the posterior cerebral vein (fig. 171, *p.c.v.*), from which a posteriorly directed branch passes caudad dorsal to the occipital column (fig. 169). A mesenchymatic tectum occipitale is present, and an occipital nerve pierces the occipital column basally (fig. 173, *occ.n.*). A rudiment of a primary postorbital process (fig. 171, *pr.po.*) is present on the lateral side of the frontal part of the auditory capsule.

Below the anterior part of the auditory capsule, immediately behind the prootic foramen and below the ramus hyoideomandibularis *VII.*, there is a "lateral commissure" (figs. 170, 171, *l.c.*). It consists of a thin lamina connected only along a short portion with the lamina basiotica. This thin lamina anteriorly bends up lateral to the ramus hyoideomandibularis and the vena capitis lateralis. Its upper part is blastematic and is connected with a blastematic layer covering the auditory capsule in this region. Posteriorly the lamina runs out in a conical rod, ending at the anterior tip of the hyomandibula.

The polar cartilages and trabeculae (fig. 171) have fused with one another. In addition, the polar cartilage is fused with the pila antotica but not with the parachordal plate. The acrochordal wings are in contact with the polar cartilage as well as with the orbital.

The polar cartilages + the trabeculae form an angle of not quite 90° with the parachordal plate (fig. 171). By means of the deep portion of the medial area (figs. 170, 171, 173, *m.a.*) the trabeculae are connected with one another in the medial line to form the trabecular plate. The connecting medial part in front of the trabecular plate extends to form a part of the floor of the cranial cavity (the rostral plate) (fig. 169, *r.pl.*) in front of the trabecular plate. This part is thus formed by the deep portion of the medial area. The other portions of this area give rise to a diffusely outlined medial keel (*m.a.*), extending from the posterior end of the trabecular plate to the frontal end of the rostral plate. At the level of the nasal opening, however, the superficial part of the medial area, is well outlined and is here seen to form a distinct swelling of the medial rostral keel (fig. 170).

Caudally, behind the hypophysial stalk (foramen) (fig. 173, *hyp.*) the trabecular plate is augmented by the precarotid and the postpituitary commissures between the polar cartilages. These commissures embrace the paired carotid arteries and join medial to them there forming an unpaired plate, which is fused with the trabecular plate anteriorly (ventrally) and meets the acro-

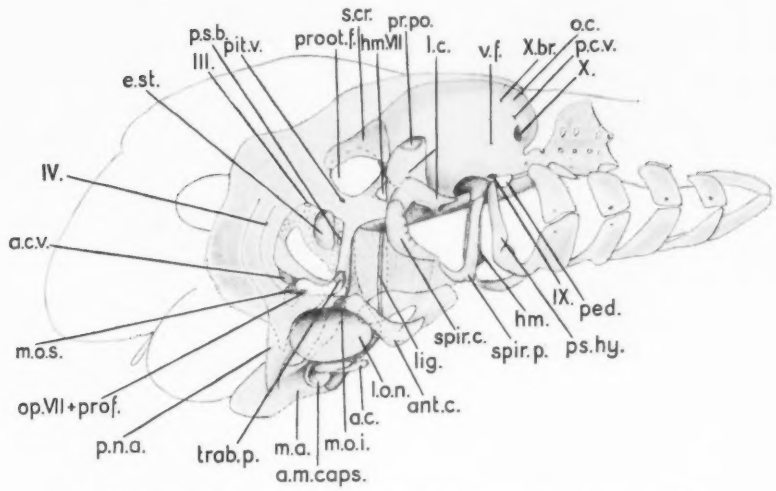

Fig. 171. *Urolophus*. 27 mm. Skull. Reconstruction. Lateral aspect.

chordal tissue posteriorly (dorsally) (fig. 169). The said unpaired plate is quite easily distinguishable from the trabecular plate, as its chondrification is less advanced than that of the latter.

The somewhat narrow foramen of the pituitary vein[1] (figs. 169, 171, *pit.v.*) has a rather peculiar position in the 27 mm *Urolophus* as it lies closely to the posterior margin of the cartilage bridge connecting the orbital cartilage with the preotic part of the basiotic lamina. This cartilage bridge should therefore consist of two components, that anterior to and that posterior to the foramen, of which the latter should be the "pila antotica", the former the "posterior sideplate" of KÄLLBERG. It seems possible that in *Urolophus* the "sideplate" arises earlier than the pila antotica. The efferent pseudobranchial artery and the oculomotor nerve are not yet enclosed in cartilage.

About midway, the trabecula has a rounded, caudally directed, short lateral process (fig. 170, 171, *trab.p.*). Into this process is inserted the musculus obliquus inferior (*m.o.i.*). From this process a broad triangular lamella extends dorsad and frontad, joining the anterior part of the orbital cartilage and forming ventrally the boundary of the optic fenestra (fig. 171). This lamella lies in front of the foramen of the anterior cerebral vein (*a.c.v.*), and immediately below this foramen it contains the insertion of the m. obliquus superior (*m.o.s.*). The lamella is thus, no doubt, the "anterior sideplate" (KÄLLBERG). As the orbitonasal lamina proper has no connection with the said lamella, one is forced to believe that that part of the lamella lying anterior to the vein foramen is an independent structure of its own. The orbitonasal vein runs anterior to the sideplate between it and the orbitonasal lamina

[1] In a 35 mm *Urolophus* the pituitary vein has disappeared on the right side.

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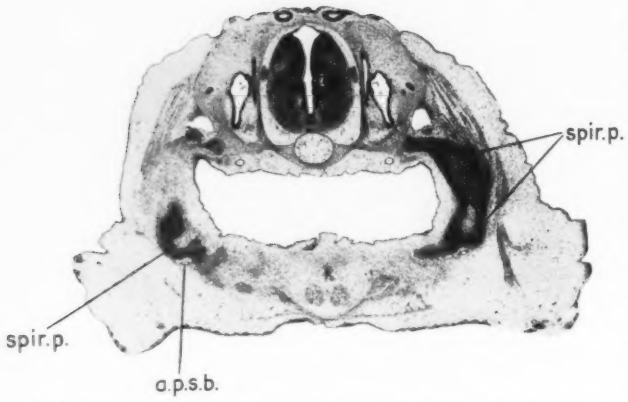

Fig. 172. *Urolophus*. 27 mm. Transverse section in the region of the posterior spiracular cartilage.

proper. In addition to this connection between the orbital plate and the trabecular process, there is another bandlike connection behind the foramen of the anterior cerebral vein (fig. 171). This connection also extends between the orbital cartilage and the trabecular process.

The orbital cartilage is well developed. It is connected with the auditory capsule posteriorly by means of a broad taenia marginalis. On its lateral side it has a crest. Lateral to this crest run the fila of the ophthalmic nerve on their way to the supraorbital sensory line. Lateral to the crest and dorsal to the foramen prooticum lies an independent blastematic rudiment, forming part of the future supraorbital crest (fig. 171, *s.cr.*). The fila of the ophthalmic nerve run medial to this rudiment or pierce it. The rudiment of the orbital cartilage is pierced by the trochlear nerve (*IV.*).

The foramen prooticum is divided by a blastematic bridge (prefacial commissure) into an anterior foramen for the trigeminal complex (fig. 171, *proot.f.*) and a posterior foramen for the hyoideomandibularis facialis (*hm.VII.*).

The lamina orbito-nasalis (*l.o.n.*) is independently established and forms the nasal capsule, dorsally, laterally and posteriorly covering the nasal sac. It has not yet fused with the trabecula, but at one point it is in contact with it. The rudiment of the lamina has a slender medial process (fig. 170, *l.o.n.*) running mediad below the trabecular plate. Medially it is connected with the thickened part of the medial area. Immediately caudal to the process the vena orbitonasalis (fig. 173, *o.n.v.*) runs between it and the trabecular plate. The anteromesial part of the future nasal capsule (figs. 170, 171, *a.m.caps.*) is formed by a blastema transversely extending from the rostral area to near the anterior end of the annular cartilage. It apparently corresponds to the "clubshaped" rudiment in *Scyllium*.

The mesenchyma of the eyebrow area is connected frontoventrally with the rostral area by a thin lamella (fig. 171, *p.n.a.*). Inside this lamella run the anterior portion of the n. ophthalmicus superficialis *VII* and profundus. The eyebrow area below the eye is obsolete for some distance. In this part, below the eye, an indistinctly demarcated tongue of mesenchyma extends to-

wards the eye. Further, caudally the area again becomes well defined, lying close to the nasal cartilage. Posteriorly it extends caudad, forming the rudiment of the "antorbital" cartilage (figs. 170, 171, *ant.c.*), which basally is pierced by a branch of the r. buccalis *VII*. Into the basal part of the "antorbital cartilage" is inserted a ligament (*lig.*) extending in front of the spiracular cartilage.

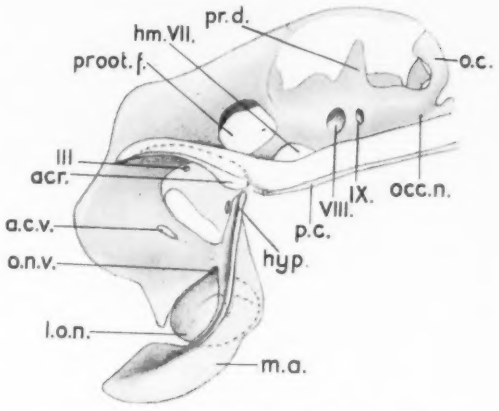

Fig. 173. *Urolophus*. 27 mm. Skull. Reconstruction. Medial aspect.

A roughly horseshoe-shaped annular cartilage (*a.c.*) surrounds the frontal part of the nasal aperture. The medial limb of the horseshoe is longer than the lateral, the lateral broader than the medial.

The mandibular and hyoid arches are less chondrified than the branchial.

The palatoquadrate and the mechelian cartilage are not yet separated (figs. 170, *md.a.*). The palatoquadrates do not reach each other in the midline, whereas the lower jaw cartilages are about to join anteriorly (mesially). The palatoquadrate portion is a somewhat bent rod without any processes. It is, however, connected by a mesenchymatic lamina with the lateral border of the trabecular plate (fig. 171). Frontally, this lamina is continuous with the blastema of the lateral process of the trabecula. The lamina lies caudally inside the anterior parts of the m. levator palatoquadrati, and posteriorly it seems to pass without any boundary into the anterior border of the blastema in which the prespiracular cartilages are developed. The system of the prespiracular cartilages consists of a blastematic lamella extending from the palatoquadrate ventrally to the rudiment of the primary postorbital process dorsally (*pr.po.*). In this lamella the prespiracular cartilage (*spir.c.*) proper exists as a cresent-shaped cartilage plate. The posterior border of this plate is crenelated by a row of 6 or 7 very short processes, which indicate that the prespiracular cartilage plate is composed of as many fused rays. The uppermost of these rays, which is not chondrified, bends in towards the otic capsule, where it is continuous with a blastema covering the otic capsule up to the separately formed postorbital process. In this lamella the "lateral commissure" is a chondrifying ventral part, perhaps derived from a prespiracular branchial ray. It has no special relation to the orbital (external carotid) artery. Closely behind the ventral end of the prespiracular cartilage another cartilage (figs. 170, 171, *spir.p.*) rod runs out, extending along the posterior lower wall of the spiracular canal and medial to the constrictor I muscle.

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This rod adheres to and fuses (31 mm stage) with the outside of the hyomandibular cartilage (fig. 172, *spir.p.*). Its lower part forms the articular process of the hyomandibula, its upper part probably corresponds to the small rudiment on the lateral surface of the hyomandibula in *Raja*. Immediately medial to the lower end of the rod the afferent pseudobranchial artery (*a.p.s.b.*) makes a dorsal bend and runs into the pseudobranch medial to the m. constrictor I. Caudally, the artery runs ventral to the lower end of the cartilage rod. In comparison with the conditions in a branchial arch one finds that the corresponding artery, the commissure between the anterior and posterior capillary net, runs ventral to the basis of the branchial ray which lies where the epi- and ceratobranchials meet. It seems very probable, therefore, that the lateral hyomandibular lamella is a mandibular ray adhering to the hyomandibula and fusing with it. Additional evidence in support of this mandibular ray theory is afforded by the general relations of the constrictor muscles. In the first branchial arch the m. constrictor dorsalis is in early stages inserted into the epibranchial. As branchial rays develop, the insertion shifts to the medium ray. In the mandibular arch (*Urolophus*) the m. constrictor dorsalis I bends lateral to the praespiracular cartilage but is never inserted into the mandibular arch. Instead it runs dorsal to the articular part of the hyomandibula and inserts into it at the point where it connects with the hyomandibula proper. The lateral hyomandibular lamella is thus, no doubt, a mandibular ray, situated on the boundary between the epi- and the ceratomandibular elements.

The hyomandibula (*hm.*) proper is rodlike and consists of a narrow dorsal horizontal part articulating against the auditory capsule and a more vertically located ventral part. The articulation head lies between the hyoideomandibular nerve and the glossopharyngeal nerve. Whether there is a ceratohyal element represented by a short mesial process at the lower end of the hyomandibula could not be determined for lack of suitable developmental stages.

Immediately lateral to the posterior end of the articular part of the hyomandibula lies the dorsal end of the pseudohyoid (figs. 170, 171, *ps.hy.*). This element is incompletely divided into two pieces, of which the lower is fused ventro-caudally with the ceratobranchial of the first branchial arch.

The branchial arches are subdivided into three wellseparated parts (fig. 171) viz. pharyngo-, epi- and ceratobranchials. The first hypobranchial (fig. 170) is also present as a rod connecting up with a medial rudiment of the first basibranchial. The other hypobranchials seem to be included in the long second basibranchial. The three first branchial arches have small separate pharyngobranchials. In the two last arches separate pharyngobranchials are not present.

Urolophus Halleri, stage 31 mm.

The anterior preotic part of the lamina basiotica has broadened considerably (fig. 174). The fissure between it and the parachordal continues caudally as a line along which the cranial floor thins out. Between the skull and the vertebral column an articulation has been established. A medial part of the parachordals surrounding the notochord has become separated from its lateral parts, the former constituting an articular plug on the vertebral column, articulating with the edge of the cranial parachordal part, the latter forming lateral articular processes on the occipital column. These are horizontally flattened and articulate with lateral ridges on the vertebral column. (Compare fig. 182).

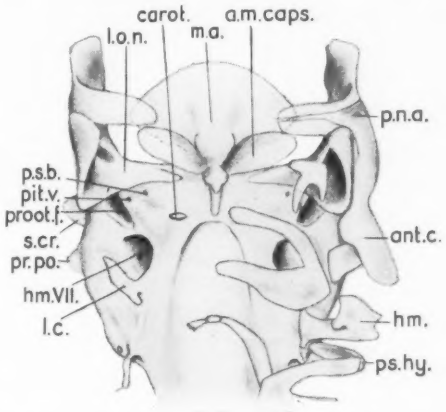

Fig. 174. *Urolophus*. 31 mm. Skull. Reconstruction. Ventral aspect.

The middle part of the auditory capsule is still very incomplete (figs. 175, 176). Its anterior and posterior divisions, however, are already roofed.[1] The nervus vagus previously resting upon the upper edge of the medial wall of the capsule (fig. 173) is now completely separated from the auditory capsule (fig. 176) by a thin lamella rising from the medial wall and reaching the roof of the auditory capsule. Below the nerve the cartilage is thickened, as in the preceding stage, the nerve thus being placed on a solid shelf. The dorsal part of the occipital column has fused with the medial lamella just mentioned and with the lateral auditory cartilage portion. The previously existing fissure between the auditory capsule and the occipital column is thus closed. However, there persist two foramina as remnants of this fissure: an upper, anterior one enclosing a nerve fibre belonging to the nervus vagus (fig. 175, *X. br.*), and a lower, posterior one enclosing the vena cerebralis posterior (*p.c.v.*). Both foramina communicate with the vagus canal. Anterior to the vagus foramen a small vein pierces the lateral wall. Its foramen in the 27 mm stage is present as a notch in the upper edge of the chondrified part of the lateral wall. Through the basal part of the occipital column run two occipital nerves (fig. 176, *occn.*) enclosed in narrow canals. The dorsomedial edges of the occipital columns are now connected by a narrow cartilaginous bridge, a tectum posterius (figs. 175, 176), which in *Urolophus* is thus the first

[1] The mesenchymatic roof laminas are omitted from the description of the 31 mm stage.

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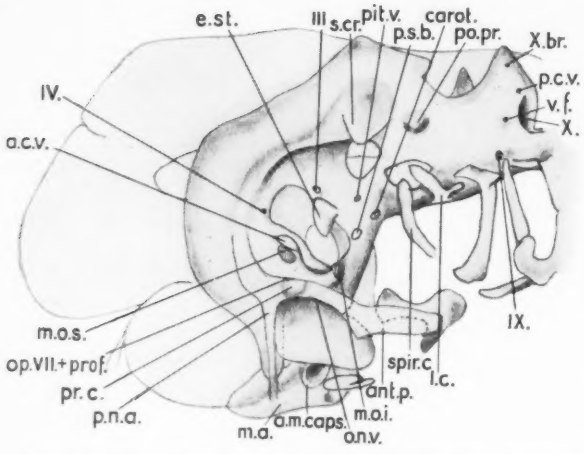

Fig. 175. *Urolophus*. 31 mm. Skull. Reconstruction. Lateral aspect.

part of the cranial roof to become established as cartilage. Besides, as in *Raja*, there are between the semicircular canals two cartilaginous bridges, of which the posterior, in *Urolophus*, continues frontad, separating the dorsal part of the posterior canal from the lateral canal. In addition to these two bridges a third is formed between the inner wall of the capsule dorsal to the lower part of the posterior semicircular canal and the thickened lateral wall dorsal to the external glossopharyngeus foramen.

The angle between the trabecular complex and the parachordals is decreasing (figs. 175, 176). The "pila antotica"—through the broadening of its prepituitary part—has become twice its former breadth. The oculomotor nerve and the efferent pseudobranchial artery have been enclosed by cartilage. The bridge between the latter and the optic fenestra is very narrow, whereas the distance between it and the foramen for the pituitary vein is very great. About midway between the oculomotorius and the efferent pseudobranchial foramina the still independent rudiment of the eyestalk (fig. 175, *e.st.*) is attached to the outside of the "posterior sideplate". The vena cerebralis anterior (*a.c.v.*) runs caudal to the anterior sideplate, the orbitonasal vein frontal to it (*o.n.v.*). That connection between the orbital cartilage and the trabecula which is posterior to the anterior cerebral vein is present as in the preceding stage.

Through apposition of mesenchyma the supraorbital crest (figs. 174, 175, *s.cr*) has broadened and its lateral border is pierced by a few ophthalmicus superficialis VII fibres. Caudally it covers the taenia marginalis laterally as a lamella. At the dorsal border of this lamella a thin, broad ventrolaterally directed lamella has arisen from mesenchymatic tissue originating at the posterior part of the upper eyebrow area. On the external surface of the auditory capsule the postorbital process, already present in the 27 mm stage, has grown stronger. Anterior to the eye the orbital cartilage is thickened, forming a preorbital ridge (fig. 175). Frontally the cartilage has grown down immediately anterior to the tractus olfactorius. The lower tip of this lamella here lies at the inner side of the frontal part of the lamina orbitonasalis but

outside the lateral margin of the rostral plate (figs. 174, 175). The connection between the lower eyebrow area and the medial area is the same as in the 27 mm stage. There is continuity between the lower eyebrow area and the "antorbital" process. Below (in front of) the eye the area is especially well defined by a denser part, which later on will form a process (fig. 175, *pr.c.*) on the preorbital ridge.

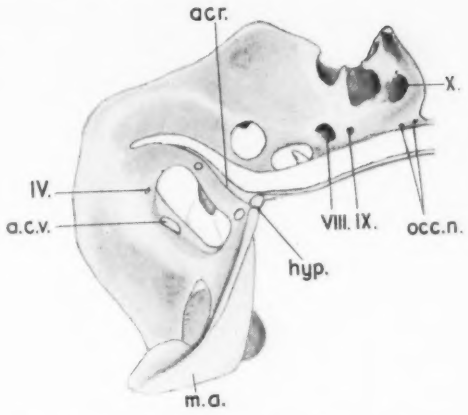

Fig. 176. *Urolophus*. 31 mm. Skull. Reconstruction. Medial aspect.

The lamina orbitonasalis is connected with the trabecular plate. The fusion has taken place through the development of a short bridge immediately dorsal to its ventromedial process (fig. 174). The orbitonasal vein runs ventral to this connection. The nervus ophthalmicus superficialis *VII* and profundus and a vein running caudad (fig. 175, *op.VII.* + *prof.*) and falling into the orbital sinus, pass between the eyebrow area and the anterior ventral part of the orbital cartilage. From the orbit they enter below the eyebrow area ventral to the anterior part of the insertion surface of the m. obliquus superior (fig. 175, *m.o.s.*) and leave the "preorbital canal" in front of the lamina orbitonasalis. An independent medial nasal capsule cartilage is present, as in *Scyllium* (figs. 174, 175, *a.m.caps.*). Beyond the posterior part of the nasal capsule the antorbital cartilage (blastema) is present as in the preceding stage.

The blastema between the hypobranchials I has developed to a small medial cartilage (fig. 174) corresponding to that in *Raja*. In other respects the visceral skeleton is principally the same as in the preceding stage. The external lamella of the hyomandibula, however, has fused with that cartilage.

Urolophus Halleri, stage about 33 mm.

The specimen of this stage has become somewhat deformed in the anterior parts of the skull, probably through some pressure from in front. A full description of these parts will therefore not be given.

The notochord, with the exception of its most posterior cranial part, is dorsally uncovered. It has lost its anterior, caudally bent, threadlike tip.

The auditory capsules are complete (figs. 177, 178). Only in the region of the ductus endolymphaticus can one look into them (fig. 177). Anterior to the foramen endolymphaticum (*f.end.*) the chondrified part of the roof of the auditory capsule extends mediad, forming the rudiments of the tectum synoticum, which have not yet met (*t.syn.*). The tectum posterius is longer

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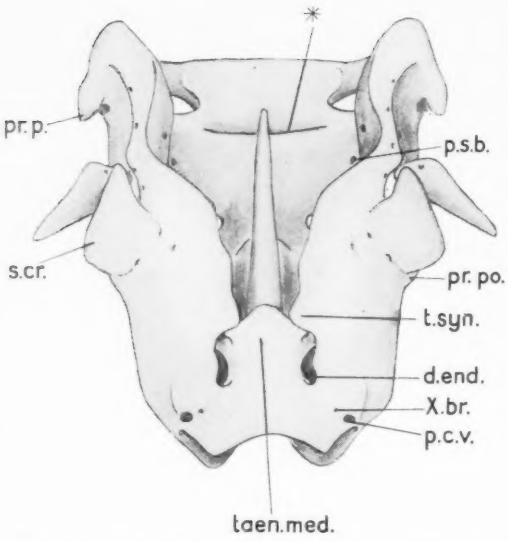

Fig. 177. *Urolophus*. 33 mm. Skull. Reconstruction. Dorsal aspect.

and a taenia medialis projects (*taen.med.*) frontad between the rudiment of the tectum synoticum. This taenia is formed by chondrification of the connective tissue lamella which in this region connects the inner walls of the two capsules with each other. A small foramen for a blood vessel has been separated from the inner glossopharyngeal foramen. In addition to the two ventral occipital nerves, piercing the basal part of the occipital column, a dorsal root corresponding to the Z of FÜRBRINGER has also been enclosed in the occipital column. The anterior cartilage bridge in the interior of the auditory capsule has lengthened posteriorly, and now encloses the dorsal part of the anterior semicircular canal in a cartilaginous canal in the roof of the capsule as in *Scyllium*. From the bridge lying dorsal to the lower part of the posterior semicircular canal, a lamella extends frontad, lateral to the canal, to fuse with the inner wall of the capsule immediately above the inner glossopharyngeal foramen, forming a short tube for the posterior semicircular canal.

The cartilage plate which is regarded here as a secondary processus postorbitalis (figs. 177, 178, *s.cr.*), and in the preceding stage was formed dorsal to the foramen prooticum has now become considerably enlarged. Anteriorly it has been extended above the eye. Posteriorly, it has fused with the primary processus postorbitalis (*pr.po.*). The "lateral commissure" is completely fused dorsally with the lateral wall of the auditory capsule, enclosing the vena capitis lateralis and the ramus hyomandibularis *VII.* in a short canal (the jugulo-hyomandibular canal). GEGENBAUR, describing such a canal in *Trygon, Pristis* and *Rhynchobatus*, thinks that the anterior orifice of the canal corresponds to the foramen of the palatinus facialis nerve in other fishes, the posterior being the foramen of the hyomandibular trunk. The ramus palatinus, it is true, runs anteriorly to the bridge and the hyomandibularis nerve behind the bridge, but the position of the jugular vein contradicts such a view. In addition, there forms later on a separate palatinus foramen in *Urolophus*. The commissure only partially corresponds to the very late chordifying lateral commissure in *Squalus*, as DE BEER has described it. In

Urolophus this canal is established much earlier. The inside of the hyomandibula articulates with the posterior rodlike part of the commissure (fig. 178, *l.c.*).

The angle between the trabecular plate and the parachordal has now disappeared completely. (In the only available specimen the trabecular plate has a sudden bend in the ethmoidal region. Probably this bend is not normal, but must be considered an artefact, the anterior part of the specimen being damaged.) The praefacial commissure has chondrified and the foramen prooticum has decreased by the forming of a lamella, connected with the pila antotica, and enclosing the abducens nerve (fig. 178, *VI.*), which thus leaves the cranial cavity through a separate foramen. The lamina orbitonasalis and the anterior sideplate have fused dorsal to the nasal sac. As a remnant of the most posterior part of the fissure between them, there is left a small foramen, through which a vein with branches upon the outside of the nasal sac leaves the nasal capsule. The orbitonasal vein in *Urolophus* goes behind the nasal capsule without piercing any cartilage caudal to the point of fusion between the lamina orbitonasalis and the anterior sideplate. The anterior border of the lamina orbitonasalis has fused with the fronto-ventral part of the orbital cartilage. The dorsal border has fused with the lateral side of the orbital cartilage immediately anterior to the nervus ophthalmicus superficialis *VII*. The lower eyebrow area of mesenchyma has fused with the orbital cartilage, forming a ridge. From this ridge has arisen a posteriorly directed processus preorbitalis (*pr.p.*) (rudiment already present in the 27 mm stage), medial and posterior to which the posterior opening of the preorbital canal is situated. This canal resembles of that in *Raja*, but in *Urolophus* it does not communicate with the nasal capsule. Its medial wall is formed by the anteroventral process of the orbital cartilage (compare the 31 mm stage, fig. 175), its lateral by the rostral process of the lower eyebrow area, which has chondrified and fused with the anteroventral process of the orbital cartilage. In the present stage the profundus nerve (fig. 178, *prof.*) leaves its canal further along frontally than the superficialis (fig. 178, *op.VII.*). The internasal septum is a broad plate, concave on its dorsal side.

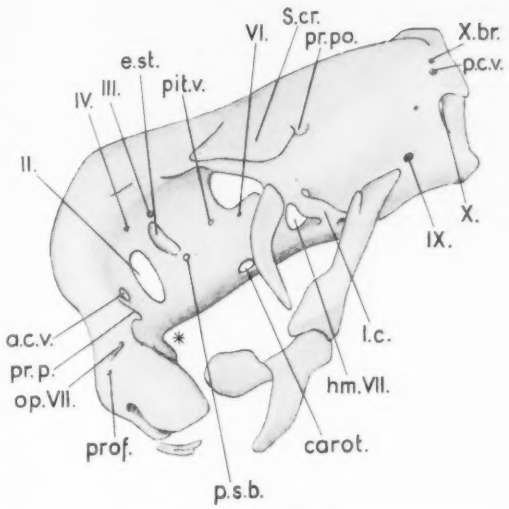

Fig. 178. *Urolophus*. 33 mm. Skull. Reconstuction. Lateral aspect.

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The anterior downwardgrowing lamella of the orbital cartilage has fused partly with the upper anterior margin of the orbitonasal plate, partly with the lateral end of the independently developed medial cartilage of the nasal capsule of preceding stages. The medial cartilage of the nasal capsule extends posteriorly, forming the anteromesial wall of the nasal capsule. The posterior medial and posterior part of the capsular wall is formed by the medial process of the lamina orbitonasalis. This process is separated from that of the other side by a short but solid nasal septum, formed by the medial area. The rostral part of the medial area could not be studied properly on the specimen available.

The mandibular arch is divided into its ordinary pieces. The palatoquadrates as well as the mandibulae meet midway, forming symphyses.

Urolophus Halleri, stage 49 mm.

In this stage chondrification has taken place in practically all parts of the skull.

The floor of the cranial cavity is complete, the fissure between the preotic part of the basiotic lamina and the parachordals being closed. Behind the ductus endolymphaticus the fissure between the auditory capsule and the taenia medialis has been bridged by a narrow cartilage lamella, causing the formation of separate foramina for the ductus endolymphaticus and the fenestra vestibuli (fig. 179). A wide fenestra in the medial wall of the capsule—earlier closed by a mesenchymatic lamella—now has been closed by cartilage. The dorsolateral border of the auditory capsule has developed into a ridge (fig. 179). The secondary postorbital process has enlarged considerably and now forms the skeletal support for a cutaneous flap extending over and behind the spiracle. It has completely fused with the primary postorbital process. The dorsal occipital foramen (Z^d) is not present in this specimen (disappeared?).

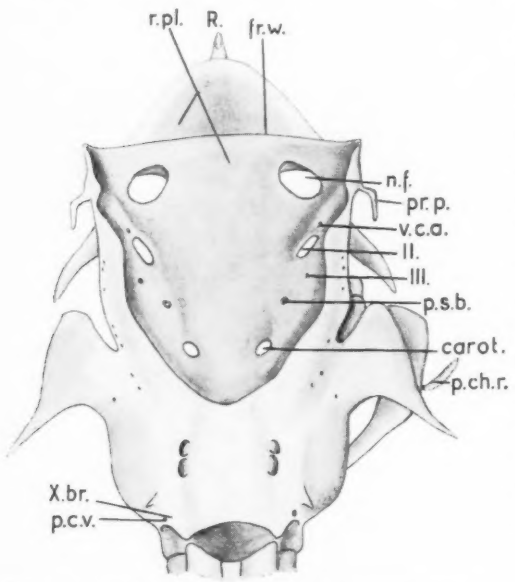

Fig. 179. *Urolophus*. 49 mm. Skull. Reconstruction. Dorsal aspect.

The straightening out of the cranial basis has apparently caused some modifica-

tions, especially in the frontal part of the skull. The floor of the cranial cavity frontally has bent dorsad, establishing a low frontal wall (fig. 179, *fr.w.*). This wall lies about in the middle of the rostral plate of earlier stages. Only the posterior part of this plate chondrifies, whereas its anterior part (figs. 179—181, *r.pl.*) remains unchondrified, forming the membranous floor of the anterior part of the brain cavity. The superficial part of the medial area (*m.a.*) belonging to the unchondrified part of the rostral plate has developed into a strong but indistinctly outlined transverse connective tissue membrane (figs. 180, 181, *m.a.*), the anterior part of which narrows considerably and ends in a small elliptical prochondrial body lying between the two medial (anterior) rays of the pectoral fins, in Trygonid rays meeting in front of the head. The nasal fenestra is horizontal (figs. 179—180, *n.f.*). The medial nasal cartilage has developed considerably, forming the medial and anterior part of the nasal capsule (fig. 180, *a.m.caps.*).

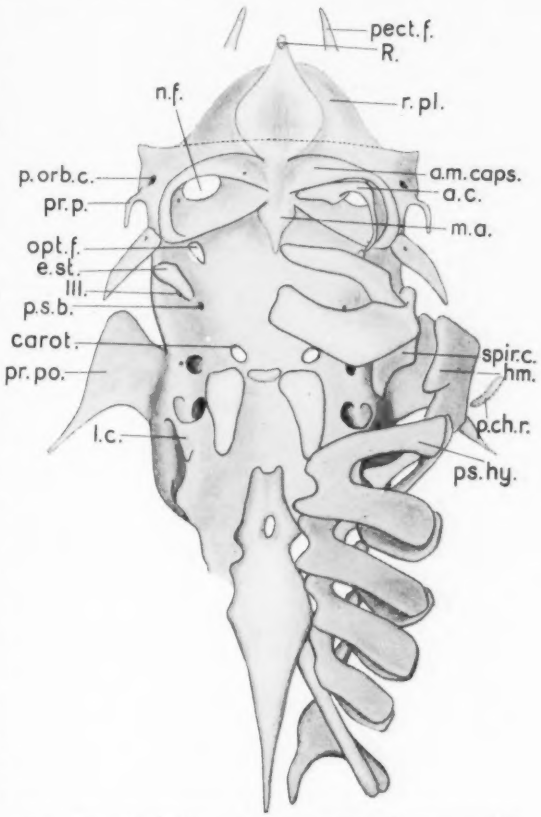

Fig. 180. *Urolophus.* 49 mm. Skull. Reconstruction. Ventral aspect.

At the enlargement of this nasal cartilage, effected by the apposition of mesenchymatic cells, a small nerve fibre belonging to the n. buccalis *VII* has been enclosed in a foramen on the lower side of the medial cartilage. The deep and intermediate part of the medial area behind the unchondrified portion of the rostral plate has developed into the solid nasal septum. Behind this septal part, the medial area is obsolete, except immediately behind it, where the superficial part of the area gives rise to a frontally broad, caudally narrow medial mesenchymatic structure the posterior part of which enters between the two palatoquadrates forming their symphysis (fig. 180). The preorbital canal is completely separated from the nasal capsule (fig. 181, *p.orb.c.*). The medial part of the annular cartilage (fig. 180, *a.c.*) has a strong

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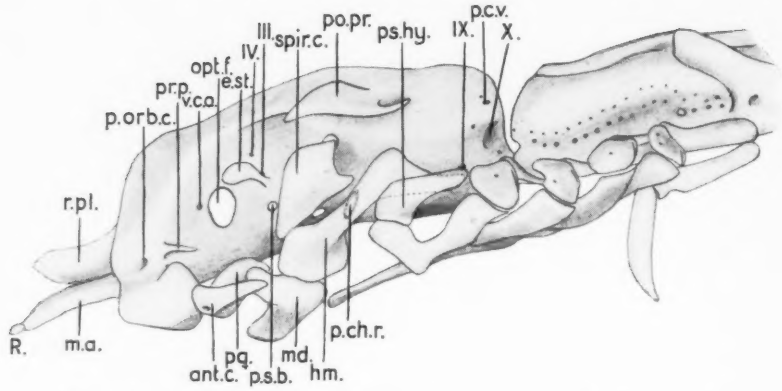

Fig. 181. *Urolophus*. 49 mm. Skull. Reconstruction. Lateral aspect.

medial and a slender lateral limb, as in preceding stages. The preorbital process (fig. 179—181, *pr.p.*) is fingerlike. The antorbital cartilage is pierced by a buccalis *VII* branch.

The mandibula posteriorly articulates with the palatoquadrate (figs. 180, 181) by means of a big frontally directed process. The prespiracular cartilage (figs. 180, 181, *spir.c.*) is a very large cartilage plate, of which the anterior lower, laterally concave, part lies in the anterior wall of the spiracular canal. This part is directed towards the lower part of the hyomandibula. The cartilage plate is connected by a ligament with the skull immediately anterior to the foramen of the r. hyomandibularis.

The lower articular part of the hyomandibula is very large (fig. 181, hm.). The fossa on the skull with which the hyomandibula articulates is short. The pseudohyoid (*ps.hy.*) rests laterally on the posterior part of the upper margin of the hyomandibula. Dorsal to the posterior dorsal corner of the hyomandibula, the dorsal ridge of its articular fossa runs out in a chondrified process (mesenchymatic or prochondrial in preceding stages). WOSKIBOJNIKOFF (1914), SEWERTZOFF (1923), and others hold it to be a pharyngohyal. Its relations to arteries and nerves make this interpretation probable. A comparison with the other rays, however, makes it very likely that it represents only the posterior part of a pharyngohyal or an interarcual. Later it fuses with the skull, causing the pseudohyoid to articulate with the skull. Posteriorly it is connected by a ligament with the first branchial epal element. Immediately behind the point where the ramus hyomandibularis *VII* bends down upon the outside of the hyomandibula, an independent and rather superficial, antero-laterally directed, prochondrial rod (figs. 179, 180, *p.ch.r.*) has appeared. It is already present in the 33 mm stage, where it is a mesenchymatic cell mass. Its significance is as yet quite obscure. GARMAN (1913) found it in *Urobatis sloani* and called it a "supraspiracular" cartilage.

From the lower ends of the ceratobranchials issue postero-medially directed processes (fig. 180). They lie ventral to the next arch. The copular plate is now a single unity. As if reminiscent of its originally paired anterior part, there is a medial foramen left in its anterior portion. The branchial rays articulate with their arches, and are not, as in *Torpedo,* fused with them.

Urolophus Halleri, stages 60 and 90 mm.

The notochord is considerably reduced. Its anterior tip in the 60 mm stage only reaches to the level of the carotid foramina. It is about to be raised up from the groove in the parachordal plate (fig. 182, *n.ch.g.*), where it formerly rested. In a 90 mm embryo the notochord has completely disappeared from the skull.

The chief interest in the 60 mm stage attaches to the nasal region. Two new posteriorly directed slender processes are present, connected with the medial part of the annular cartilage (fig. 183, *a.c.*) Between them lies a small separate cartilage, and medial to them a somewhat larger one. In the 90 mm stage a number of new small prochondrial pieces have arisen in the nasal flap. The posterior end of the slender lateral process of the annular cartilage is bent mediad and frontad. Against this frontally directed part rests a small cartilaginous rod. (The structures described are best understood if a comparison is made between figures 183, 184.) Midway between the nasal capsules are found two cartilaginous elements, of which the anterior. V-shaped, is frontally unpaired, but caudally extends in two diverging legs, one dorsal (posterior) to each nasal sac. The posterior element is that part of the superficial portion of the medial area which has been described in earlier stages. The anterior cartilage contains a sensory tube, and is a sensory tube cartilage (fig. 183, *scns.c.*). HASWELL (1884) describes the anterior of these cartilages in *Urolophus sp.,* stating that its existence constitutes the main difference between the skulls of *Urolophus* and *Trygon.* According to him it is either a labial cartilage or a rostrum remainder. GEGENBAUR (1872) illustrated in *Trygon* a small unpaired cartilage,

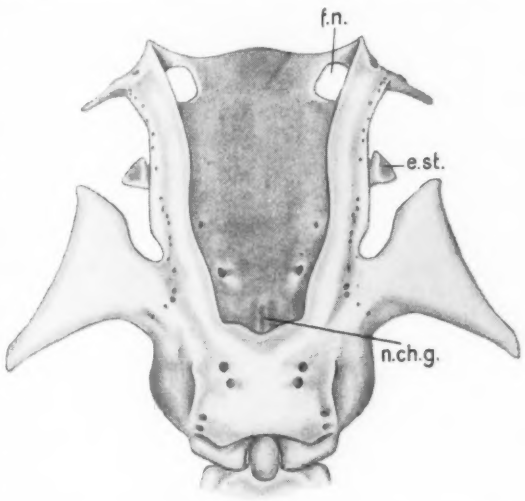

Fig. 182. *Urolophus.* 60 mm. Skull. Reconstruction. Dorsal aspect.

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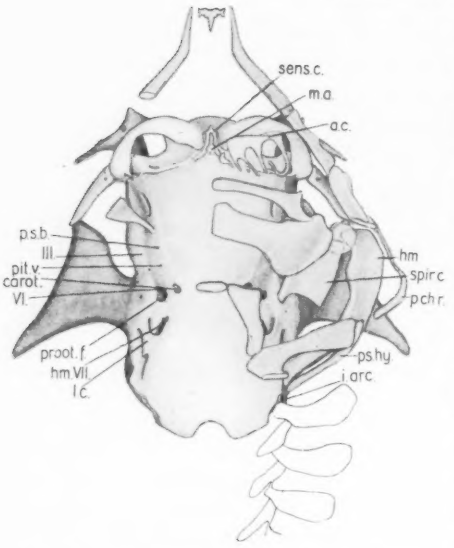

Fig. 183. *Urolophus.* 60 mm. Skull. Reconstruction. Ventral aspect.

which could be taken for two fused labial cartilages. It corresponds to the posterior cartilage (fig. 183, *m. a.*) in *Urolophus.* Its equivalent in *Myliobatis,* according to FÜRBRINGER (1913), is cleft posteriorly, but not so deeply as in *Urolophus.* It corresponds to the anterior cartilage. In *Torpedo* an unpaired cartilage (the raphe) is present. It corresponds to the "Lippenträgerknorpel" of J. O. MÜLLER and not to the V-shaped cartilage in *Urolophus.* On the contrary, the equivalent to the "Lippenträgerknorpel" is the posterior, ventral cartilage in *Urolophus.* It is pierced by a glandular tube. In the 90 mm stage it is differentiated into a vertical lamella, of which the lower border extends to form anterior and posterior processes (fig. 184, *m.a.*). Neither in *Urolophus* nor in *Torpedo* is its early rudiment paired, and it could scarcely therefore be taken for fused labial cartilages. The same applies to the anterior V-shaped cartilage in *Urolophus.* It does not consist of two solid cartilaginous rods, as HASWELL seems to have assumed, but in this stage forms a deep gutter enclosing the infraorbital sensory canal of the nasal region of the head. In the 90 mm stage the gutter has partially closed to form a tube (fig. 184, *sens.c.*). Each leg of this cartilage thus corresponds to the paired "upper labial cartilage" in *Raja,* which is a sensory line cartilage, although as has been explained before it does not enclose the sensory canal. At the tip of the V lies the crosscommissure between the canals of both sides. No labial cartilages are present in *Urolophus.* The rostral rudiment between the anterior tips of the pectoral fin skeleton in the 60 mm stage is T-shaped (fig. 183). To judge from the structure of the cartilage the cross-stroke of the T seems to be produced by the

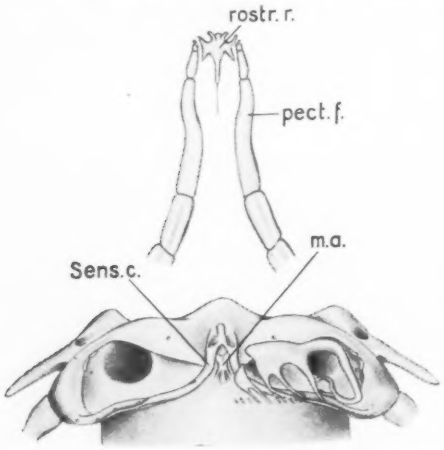

Fig 184. *Urolophus.* 90 mm. Skull. Ethmoidal part. Reconstruction. Ventral aspect.

fin skeleton. In the 90 mm stage it is clearly seen that the formation of new cartilage elements takes place at the tip of the pectoral fin (fig. 184). In the 90 mm stage the rostrum rudiment has a number of processes radiating from a central disc. The anterior border of the skull in the midline bulges out somewhat, to form a sort of short and broad rostral process (fig. 182, 184), answering to the unchondrified part of the deep portion of the rostral plate. The superficial portion has been transformed into a strong transverse ligament. Its anterior tip is the rostral rudiment described in the preceding lines.

Between the lower jaw and the hyomandibula a big pad of fibrous tissue, forming a quadrato-hyomandibular ligament, has grown (fig. 183) larger. It is present in the 49 mm stage. The prespiracular cartilage (fig. 183, *spir.c.*) now occupies a more horizontal position in the roof of the spiracular canal. The cartilage rod (fig. 183, *p.ch.r.*) on the outside of the hyomandibula of the preceding stage now runs out stringlike in a cutaneous fold below the spiracle. In front it is connected with the prochondrial tube enclosing the postorbital sensory line. Perhaps the rod is a derivate of the envelope of the sensory line.

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Behind the pharyngohyal a small cartilage has formed corresponding to the cartilage X illustrated by WOSKIBOJNIKOFF in *Rhinobatus*. It lies almost at the anterior border of the epibranchial I and in the ligament connecting the pharyngohyal with the epibranchial I. Medially to the cartilage runs the ramus palatinus IX. In the branchial arches the pharyngobranchials have a small posterolateral process running along the ligament connecting the pharyngobranchial with the next epibranchial. Between the process and the pharyngobranchial proper runs the ramus palatinus *X*. In the first branchial arch the tip of the process is fused with the pharyngobranchial proper dorsal to the nerve, which thus pierces the cartilage. From these conditions it seems possible to conclude that the second small cartilage of the hyoid arch corresponds to a similar posterolateral process of the pharyngobranchials, i.e. to an interarcual.

GENERALITIES IN THE DEVELOPMENT OF THE SKULL IN SHARKS AND RAYS.

So far as can be ascertained, sharks and rays behave similarly in regard to the early and earliest differentiation of the mesoderm (mesenchyma) of the head. It is supplied partly from the heads somites, partly from the neural crest.

From the vesicle of Platt (if present) and the premandibular somite there result: 1. the eye stalk, 2. a posterior part of the orbital wall, 3. parts of the sclerotic membrane of the eye and 4. perhaps part of the trabecula.

From the walls of the mandibular somite there originate: 1. the acrochordal

tissue with the antotic cartilage (pila antotica), 2. the polar cartilage and 3. in *Squalus* and probably in the other selachians a part of the meninges in the region of the plica encephali ventralis.

The hyoid somite provides: 1. the anterior portion of the parachordal, 2. the anterior part of the basiotic lamina with the anterior basicapsular commissure, and 3. probably the anterior (preglossopharyngeal) part of the medial wall of the auditory capsule.

From the glossopharyngeal somite there result: 1. a posterior portion of the parachordal, 2. the posterior part of the basiotic lamina with the posterior basicapsular commissure, and 3. probably the posterior part of the inner wall of the auditory capsule.

The first postglossopharyngeal somite gives rise to: 1. a portion of the parachordal and 2. the occipital column (when not consisting of more than one segment).

All other parts of the skull seem to arise from the neural crest (ecto-mesoderm).

The differentiation of the neural crest mesenchyma seems to take place successively by delamination of cell laminas. In very young stages the sides of the head, inside the epithelium, are covered with a layer of mesenchymatic (ecto-mesodermal) cells. This layer soon becomes differentiated in such superficial fields which have been described in early stages of *Squalus*, and which are stated to be present in all the selachians studied. Deep parts of this mesenchyma "sink in" towards the brain to form certain parts of the cranial skeleton (and a part of the meninges). In this way the rudiments of the orbital cartilage with the medial part of the taenia marginalis, at least the anterior part of the trabeculae, the "trabecular commissure" and the rostral plate, and the dorsal and lateral parts of the auditory capsule, are formed as a first set of cranial parts. By this "sinking-in"-process, however, a superficial part of the mesenchyma is left inside the skin. This mesenchyma is chiefly used up in forming connective tissue parts of the head, but in that part also skeletal structures arise by "sinking-in" of portions of mesenchymatic tissue. The supraorbital crest cartilage, the primary processus postorbitalis, the preorbital cartilage and the lamina orbitonasalis and its dependents are, as a result of this second process, added to the cranial rudiment. To a third set of skeletal structures apparently belong the antorbital cartilage and a mesenchyma connecting up with the rostrum and containing, in rays, the rostral appendix.

After the second and third delaminations, mesenchymatic tissue is left below the skin. This portion also contains cells possessing the property of forming skeletal tissue, wiz. placoid scales and envelopes of sensory canals, some of which (in the anterior part of the skull) may chondrify, especially in rays. In *Chimaera* (and Teleostomians) ossification occurs in such envelopes.

The different, cell-laminas are connected with one another by laminas of scattered mesenchymatic cells. These laminas are likewise able to form skeletal tissue. This is well demonstrated at points where the skeletal elements differentiated in different mesenchymatic layers fuse with one another, and also where the embryonic cartilages grow thicker.

Thus, all parts of the ecto-mesoderm of the neural part of the skull (occasionally) have the property of chondrifying.

This statement has its peculiar interest if a comparison is made with the conditions in certain Cephalaspids, in which STENSIÖ has demonstrated a massive continuous skeletal tissue (bone or mucous cartilage) forming the neural cranium and extending outwards to the skin.

Another conclusion, which partly follows from the successive formation of the neurocranial components of *Squalus* (and the other selachians), as outlined above, is that the various parts of the skull are formed in situ. At a certain stage the skull is modelled in mesenchymatic matter. In this model chondrification may take place in the different parts simultaneously. The main parts that originate fram the first delamination, however, seem to chondrify earlier than those of the second. But this is not always the case, as membranes connecting parts of a certain layer may chondrify later. Chondrification always takes place in already preformed membranous or condensed mesenchymatic parts. A mesenchymatic or membranous skull thus always precedes the cartilaginous.

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THE POSSIBLE SIGNIFICANCE OF THE MESENCHYMATIC AREAS IN THE HEAD OF THE SELACHIAN EMBRYOS.

In the 24.5 mm stage of *Squalus acanthias* the only skeletal elements that have chondrified, or, at least, are about to chondrify, are the parachordals. Most other elements, however, are present as blastematic or procartilaginous rudiments. The foregoing description of the development made it possible to show that there is a relation between the subepidermal mesenchymatic areas and the principal structures of the future skull. As such areas are present in other sharks, and also in rays, it is at least possible that they were present also in the common ancestors of those fishes. From such superficial ecto-mesenchymatic areas most parts of the skull develop by means of successive delaminations. The remnants of the areas are left as diffuse connective tissue between the epithelium and the skeletal parts, or as bands of modified connective tissue underlying the lateral sensory lines. As the sensory lines develop into mucous tubes, this tissue forms the half cylindrical envelopes of those tubes. These envelopes correspond closely to those that exist around the sensory line tubes in holocephalians, ganoids and bony fishes,

where they contain the matrices of the sensory line bones which, together with adjoining connective tissue, form the main part of the dermal bones.

If one accepts the view that in sharks the ontogenetical cranial development reflects general traits of the phylogenetical development of the vertebrate cranium, it would not be impossible to believe that the ontogenetical stage during which the ecto-mesoderm is not yet differentiated corresponds to a phylogenetical stage when skeletal tissue filled the entire space between the skin epithelium and the brain, surrounding the nerves and blood-vessels. Such a skeletal tissue could not be determined either as exo- or as endoskeletal. In Cephalaspids, according to STENSIÖ, there is present a cranium that may correspond to such an undifferentiated ontogenetical stage.

From the preceding description it seems possible to conclude that the formation of the non-somitic parts of the selachian skull takes place stepwise. The formation of the different elements of the skull is related to the different mesenchymatic areas as described in foregoing pages. After furnishing the material of the endoskeleton, the areas are not devoid of cells capable of forming other skeletal structures.

The differentiation of the mesenchyma in subepithelial areas seems to proceed simultaneously with the development of the lateral sensory lines and other placodes. Different structures arise from the different areas, but this differentiation does not involve the disappearance of the area or any essential changes of it. It seems therefore reasonable, to suppose that the primary areas are of fundamental and phylogenetical importance. If the principles of the development of the endocranium in the ganoid fishes, for instance, were the same as in selachians, which is quite possible, the mesenchymatic areas that are left after supplying the material to the endocranium have a relation to the formation of the exocranium, external to the endocranium. In selachians the exocranial mesenchyma of the areas contains the sensory line envelopes and furnishes material for the development of the placoid scales of the head. Thus the areas may have been related to an exoskeleton that was once present with skeletal plates corresponding in principle to the mesenchymatic areas present in young selachian embryos.[1] If we assume this possibility as a working hypothesis, the following deduction may be drawn. What would a selachian with an exocranium composed of bones corresponding to the mesenchymatic areas of the embryo look like? The figure 185 A, composed by using especially the (16.5), 22 and 24.5 mm stages of *Squalus* as guides, gives an idea of the appearance of such an exocranium. In this imaginary figure the boundaries between the bone plates surrounding the eye are somewhat arbitrary. The following explanation is necessary to enable the reader to understand how this figure has been constructed.

[1] In extinct archaic fishes the dermal bones are frequently broken up into placoid scales or small bone plates.

The frontal supraorbital plate (upper eyebrow area, *u.e.a.*) extends towards the epiphysis as in the *22* (16.5 and 24.5) mm stage. The posterior supraorbital or postorbital area (*p.orb.a.*) is characterized by the meeting point of the postorbital sensory line and the otical line divisions. Experience teaches that this point in fishes nearly always lies in a bone of its own. (dermosphenoticum). In addition, this plate lies outside the postorbital process. The big posterior part of the infraorbital bone (lower eyebrow area, *l.e.a.*) is a conclusion of the development in the 16.5, *22* and 24.5 mm stages of *Squalus*. Its narrower anterior part is from stage *22*. The preoral (*p.o.a.*) and internasal (*i.n.a.*) fields are from stages *22* and 24.5 mm. The prenasal (postnasal *po.na.*) field comes from the *22* mm stage, combined with the 24.5 mm stage, in which the bend of the sensory line enters the corresponding field. The frontal (*fr.a.*) and epiphyseal (*e.p.a.*) fields come from all three *Squalus* stages. The big parietal plate (*p.a.*), extending over the dorsal midline of the head, is given an arbitrary form, but the sensory lines adorning it are according to the *22* mm stage, the posterior end of the supraorbital line and the upper end of the postorbital line[1], of which the short end-portions lie in the supraorbital area, have been drawn out dorsally to converge against the dorsal midline as they actually do in the *22* mm stage. The two short sensory lines behind the converging point of the supraorbital and postorbital lines represent the middle and posterior pitlines respectively, of which the anterior is innervated from the glossopharyngeal, the posterior from the vagus nerves. These pitlines are taken from stages *22* and 24.5 mm. The position of the foramen endolymphaticum (*d.end.*) is in accordance with the aforementioned stages. The position of the posterior sensory line commissure is taken from the *22* mm stage. The other sensory lines are inserted according to the conditions in stage *22* and 24.5. The plate (*e.f.a.*) traversed by the otical sensory line is from the 16.5 and *22* mm stages. And, finally, the toothplates of the palatoquadrate and the mandibula are from the *22* and 24.5 mm stages.

The external form of the head in fig. 185 A is quite arbitrary, but for the sake of comparison with fossil elasmobranch fishes it has been given a form answering to that of Arthrodirans, such as, for instance, *Coccosteus* and *Pholidosteus*. Furthermore, the shape, — when arbitrary, — of the different plates of the figure has been suggested from conditions in these Arthrodirans. But the relations between the different plates and those between the plates and the sensory lines are not arbitrary, as they are based upon the actual conditions in the *Squalus* embryos. Comparing this picture with that of a reconstruction of an arthrodiran head, one is struck by the fact that the plates are arranged in a corresponding way and with similar rela-

[1] This upper end probably has some special significance, as will be demonstrated in a following part of this work.

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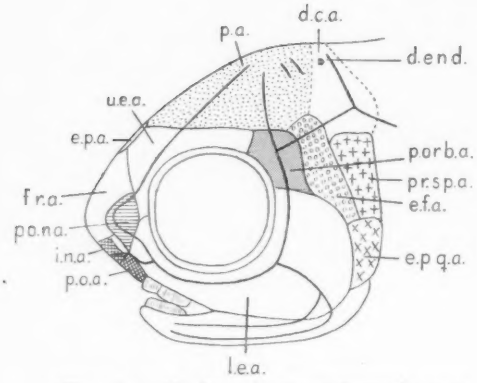

Fig. 185 A. Embryonic mesenchymatic areas of the head, diagrammatically outlined on an adult fish head.

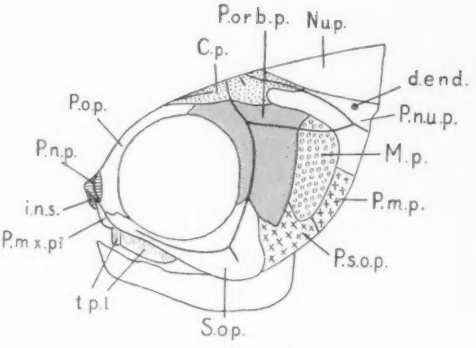

Fig. 185 B. Exoskeleton of Pholidosteus (Stensiö).

tions to one another and to the lateral sensory system. The plates illustrated correspond to mesenchymatic areas in the head of the shark embryo, areas which give rise 1:0 to the ectomesodermal parts of the skull, and 2:0 to the periferal connective tissue and the envelope of the sensory lines, which in other fishes are the sources from which the exoskeleton arises. Thus it seems possible that the selachian fishes are derived from fishes with a cranial exoskeleton arranged like that of the Arthrodirans. In the embryological development I could not find any distinct landmark for a differentiation of mesenchymatic areas of the skull behind the parietal area described above. Such areas may be sought for dorsal to the branchial arches along the lateral line, and there are undoubtedly mesenchymatic areas present, but they evidently lie behind the posterior limit of the dorsal part of the skull, and therefore have not been considered in the present paper. The fact that the branchial region of sharks shortens during ontogeny and that a sort of gill-cover is developed in *Chlamydoselachus* may be taken as evidence in support of the view that the ancestors of selachians had their branchial region covered by a gill-cover, as is the case in *Chimaeroids*, where, however, the embryo has as long a branchial region as the shark embryo. These considerations, which are further supported by the distribution of the mesenchymatic areas in the shark embryo, similar to the distribution of bone elements in the arthrodiran skull, make it probable that the skull of the shark ancestors was built in much the same way as in Arthrodirans, such as *Coccosteus* (fig. 185 C) and *Pholidosteus* (fig. 185 B). The fact that a spiracular canal has never been recognized in Arthrodirans, whereas the selachians always have one, constitutes a difference of no great importance, as in Chimaeroids, in which spiracles are missing, the embryos have well-developed spiracular clefts, similar to those of the selachian embryos. The selachians could very well

be derived from elasmobranch fishes without a typical spiracle, or from fishes in which there was a full-sized mandibular gill cleft. See part III of this work.

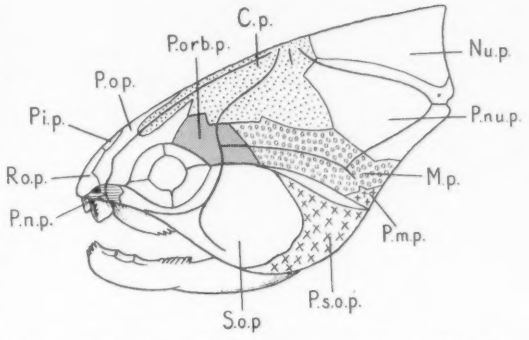

Fig. 185 C. Exoskeleton of Coccosteus (Heintz).

In the preceding lines it has been suggested that the different mesenchymatic areas of the *Squalus*-embryo may have their representatives in certain dermal bone elements in Arthrodirans such as Coccosteids. There is, however, one typical bone in the Arthrodiran dermal skull, which in *Squalus* seems to have no corresponding mesenchymatic area, viz., the postsuborbital plate. In the picture (fig. 185 A), however, this plate has a representative at *e.p.q.a.* But the plate *e.p.q.a.* is not put into the drawing quite without evidence. The corresponding postsuborbital plate in the Arthrodiran *Leiosteus* (and others) is especially characterized by its relation to the palatoquadrate of this fish. As JAEKEL and STENSIÖ (1934) have demonstrated, the posterior end of the palatoquadrate is intimately connected with the inside of the postsuborbital. In *Etmopterus,* as described earlier, on the lateral side of the posterior part of the palatoquadrate lies a blastema of rather large dimensions, which later fuses with the palatoquadrate (forming its external otic process). Outside this blastema is a subepithelial mesenchymatic disc. It seems possible that the inner blastema corresponds to that part of the palatoquadrate which in *Leiosteus* is attached to the postsuborbital. If such is the case, the outer blastema might correspond to the postsuborbital proper. It is true that in *Leiosteus* the mandibula articulates against the superficial part of the palatoquadrate attached to the postsuborbital plate, and that this is not the relation between the mandibula and the blastema in the *Etmopterus* embryo. In *Raja,* however, where a similar blastema is present, this blastema extends so far caudad that it enters, or at least borders on, the articular disc between the palatoquadrate and the mandibula. To sum up, it must be admitted that there is a great resemblance between the arthrodiran and the selachian conditions, a resemblance which may perhaps be regarded as sufficient evidence to justify the inclusion of a postsuborbital in the picture.

The preceding arguments have been given to show that the comparison between the mesenchymatic areas of the selachian embryo and the exoskeletal plates of the Arthrodirans is not so fantastic as might appear at first sight. Perhaps the presence of the areas could be used as an argument for the opinion that the selachians once had an exoskeleton of the head more or

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less of arthrodiran type, but at present quite reduced or broken up into placoid scales.

If the above deductions are correct, the following homologies could be established. (Compare fig. 185. A. Band C.)

Selachians.	*Arthrodians.*
Frontal area, fig. 185 A. *fr. a.*	Rostal plate, fig. 185 C. *Ro.p.*
Internasal area, fig. 185 A. *i.n.a.*	Internasal septum, fig. 185 B. C. *i.n.s.*
Preoral area, fig. 185 A. *p.o.a.*	Premaxillary plate (?), fig. 185 B. *P.mx.p.?*
Postnasal area, fig. 185 A. *po.na.*	Postnasal plate, fig. 185 B. C. *P.n.p.*
Epiphysial area, fig. 185 A. *ep.a.*	Pineal plate, fig. 185 C. *Pi.p.*
Upper eyebrow area, fig. 185 A.*u.c.a.*	Preorbital plate, fig. 185 B. C. *P.o.p.*
Postorbital area, fig. 185 A. *p.orb.a.*	Postorbital plate, fig. 185 B. C. *P.orb.p.*
Parietal area, fig. 185 A. *p.a.*	Central plate, fig. 185 B. C. *C.p.*
Lower eyebrow area, fig. 185 A. *l.c.a.*	Suborbital plate, fig. 185 B. C. *S.o.p.*
Extrafacial area, fig. 185 A. *e.f.a.*	Marginal plate, fig. 185 B. C. *M.p.*
Prespiracular area, fig. 185 A. *pr.sp.a.*	Postmarginal plate, fig. 185 B. C. *P.m.p.*
Extra palatoquadrate area, fig. 185 A. *e.pq.a.*	Postsuborbital plate (and internal?), fig. 185 B. C. *Ps.o.p.*
Dorso-caudal field with endolymphatic orifice and transversal sensory canal, fig. 185 A. *d.c.a.*	Paranuchal plate, fig. 185 B. C. *P.nu.p.*
?	Nucal plate, fig. 185 B. C. *Nu.p.*

To supplement this comparison it may be stated that there are in *Squalus* embryos two tooth-plates on the palatoquadrate and one on the mandibula, corresponding respectively to the two superognathals and the one inferognathal in Arthrodirans.

THE SQUALOID AND GALEOID TYPES OF SKULL DEVELOPMENT.

From the descriptions given in the preceding pages it is obvious that in the squaloid and galeoid sharks the development of the neural cranium is in many parts rather differently organized.

1. The notochordal hook disappears early in *Scyllium*, but is retained longer in *Squalus* and *Etmopterus*.

2. The parachordals in *Scyllium* are much broader than in the Squaloids. This condition in *Scyllium* corresponds to the broad and flat basis cranii of this genus (and of the other galeoid sharks).

3. The trabeculae in *Scyllium* arise as short rudiments with the rudiment of the anterior lateral process (cranio-quadrate process) at their frontal ends. Those of *Squalus* and *Etmopterus* consist of a portion behind the lateral process and a portion in front of it. Thus, the process lies at about the middle of the trabecula. As this process marks the point at which the orbital

articulation of the palatoquadrate will later develop and the trabecula in *Scyllium* does not grow out very much anterior to the process, whereas in the Squaloids the growth principally takes place frontally, these conditions are responsible for the very different position of the orbital articulation in *Scyllium* and in the squaloids.

4. In *Squalus* and *Etmopterus* the hypophysial fenestra closes early, especially from in front, by the longitudinal uniting of the trabeculae by means of the medial area. The precarotid commissure, which forms the posterior boundary of the fenestra, does not broaden very much. In *Scyllium* the polar fenestra closes rather late. The closure is effected by the trabeculae and the deep part of the medial area as well as by the precarotid commissure. Thus, the fenestra closes from in front as well as from behind and from the sides. The last traces of the fenestra therefore are rather distant from the carotid foramen in *Scyllium*.

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5. On the cranio-quadrate connecting process (lateral trabecular process) in *Scyllium* an apical portion chondrifies separately and fuses with the palatoquadrate forming its orbital process. In *Squalus* and *Etmopterus* the orbital process is formed as a process at the anterior end of the embryonic palatoquadrate.

6. The dorsal part of the prootic fenestra in *Squalus* and *Etmopterus* closes completely. In the corresponding part in *Scyllium* by the closure foramina are left for the nervus ophthalmicus V and VII and the III—V commissure. The ophthalmic nerves in the squaloids thus go through the ventral portion of the fenestra.

7. The anterior sideplate in *Squalus* and *Etmopterus* lies in the frontal continuation of the trabeculae, forming but a small angle with those parts of the basis cranii. Later, the angle grows more pronounced, as the sideplate develops forming the orbital wall portion in front of the optic fenestra. In *Scyllium* the sideplate stands perpendicular to the trabecula already at an early stage of development (27.5 mm stage). This condition seems to be a consequence of the short part of the trabecula in front of its lateral process.

8. The orbitonasal plate in *Squalus* and *Etmopterus* posteriorly forms the big ectethmoid process, frontally the lateral wall of the nasal capsule, and dorsally a part of the anterior frame of the orbita in front of the orbitonasal and the profundus foramina. In *Scyllium* the orbitonasal lamina develops but a very small ectethmoid process[1] (if any), but it forms the lateral wall of the very large nasal capsule, of which the caudal portion represents part of the orbital frame in front of the orbitonasal vein.

9. In *Scyllium* the membrane connecting the palatoquadrate with the trabecula medially chondrifies, forming the subocular cartilage or shelf. In *Squalus*

[1] In *Carcharinus mossambicus* a long ectethmoid is present in the adult.

and *Etmopterus* no such shelf is present, the connecting membrane never chondrifying.

10. In the caudal continuation of the subocular shelf in *Scyllium* there follows early a shelf portion, pierced by the orbital artery. No quite, corresponding shelf portion is present in embryos of *Squalus* and *Etmopterus,* but it develops later.

11. In *Scyllium* (31 mm) the "suprarostral process" issues from the upper border of the internasal septum in a frontal direction. In later stages an antero-dorso-mesial part of the nasal capsule develops in connection with this process. In *Squalus* and *Etmopterus* the corresponding part of the medial area already at an early stage forms a broad plate, on which in early stages the frontal part of the brain rests, and which later forms the bottom of the precerebral fossa.

12. The lateral rostral rods in *Scyllium,* developing from the antero-mesial edge of the lamina orbitonasalis, have no corresponding part in the squaloids.

13. In *Scyllium,* owing to their extensive development the nasal capsules surround the nasal fenestra on the medial, anterior and lateral sides, leaving the medioventral side open[1] (nasal fenestra). In *Squalus* and *Etmopterus* the nasal capsules occupy only the anterior part of the nasal fenestra, a posterior subnasal fenestra being cut off. This latter fenestra is the basal communication of GEGENBAUR (ectethmoid fossa of ALLIS).

14. In *Scyllium* the medial rostral rod consists of the superficial portion of the medial area, in *Etmopterus* the short rostrum is formed by the intermediary and superficial portions of this area. In *Squalus* the deep portion also takes part in the formation of the rostrum.

15. The eyebrow area of mesenchyma frontally sends down a process in front of or outside the frontal part of the nasal capsule in *Squalus* and *Etmopterus.* This process later forms the lateral wall of the ethmoidal canal of Gegenbaur. In *Scyllium* no such part occurs, so that there is no ethmoidal canal either.

16. In *Squalus* and *Etmopterus* a separate rudiment of a *primary* postorbital process is formed. In *Scyllium* the process is formed as the posterior part of the supraorbital crest rudiment.

17. In *Squalus* and *Etmopterus,* especially in the latter, the medial area forms a very strong medial keel, on about a level with the middle of the orbita. In *Scyllium* no such keel occurs.

18. In *Squalus* and *Etmopterus* a separate cartilage of KÄLLBERG arises, in *Scyllium* probably not.

From this comparison it results that *Squalus* and *Etmopterus* differ from *Scyllium* in a great number of important characters. Offsetting these points

[1] This side is closed by membrane.

of difference, however, there is a very considerable measure of agreement in the general type of development, the different elements developing from corresponding rudiments. But in the subsequent development the two shark types diverge very considerably, as shown in the preceding paragraphs. The divergence is in fact so great that it is difficult to point out differentiated characters common to the two groups. Such characters are the following.

1. The parachordals are pointed frontally.

2. The polar cartilages are not fused directly with the parachordals, but by means of an acrochordal portion, to which the pila antotica also are joined.

3. The notochord, of which the anterior end degenerates, is enclosed by the parachordals, which overgrow it dorsally as well as ventrally.

4. There is no appreciable preotic part of the lamina basiotica.

5. The braincase is closed dorsally by a tectum occipitale, a tectum synoticum, (a tectum orbitale) and an epiphysial bridge.

6. A prefrontal fontanella is present.

7. A supraorbital crest, caudally connected with the auditory capsule, is present.

8. A preorbital canal occurs.

9. The anterior sideplate lies in front of the foramen for the anterior cerebral vein and behind the orbital foramen for the orbitonasal canal.

10. Presence of an eyestalk or at least a rudiment (*Scyllium*) thereof.

11. The membranous "antorbital cartilage" (rudimentary in *Scyllium*).

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THE BATHOID TYPES OF NEURAL SKULL DEVELOPMENT.

The bathoid fishes here under consideration belong to three different families viz. the Rajids, the Dasybatids and the Torpedids. As these families are well separated it might be expected that the development of the neural skull would also present corresponding differences. In the following lines the more important differences are enumerated:

1. The anterior sideplate lies behind the anterior cerebral vein foramen and the foramen for the orbitonasal vein in *Raja* and *Torpedo*. In Urolophus the sideplate seems to consist of a bandlike portion joining the orbital cartilage behind the foramen for the anterior cerebral vein, and of a broad anterior branch joining the orbital cartilage in front of the vein. The foramen for the orbitonasal vein in *Urolophus* lies in front of this branch.

2. The lamina orbitonasalis in *Raja* and *Urolophus* forms the nasal capsule, of which the early rudiment does not reach the rudiment of the orbital cartilage. In *Torpedo* the early rudiment of the nasal capsule reaches the orbital cartilage in front of the anterior cerebral vein.

3. In *Raja* and *Urolophus* a preorbital canal is formed by the chondrifica-

tion of a small portion of the eyebrow area of mesenchyma, at the upper border of the lamina orbitonasalis. In *Torpedo* no canal seems to be formed, but a preorbital process (answering to the fingershaped process in *Urolophus*) develops in the corresponding place.

4. In *Raja* the ethmoid nerve becomes enclosed in the nasal capsule, leaving it anteroventrally. In *Torpedo* and *Urolophus* the nerve passes outside the capsule.

5. In *Raja* a strong rostrum is developed. In *Urolophus* the rostrum is represented by a small cartilage developing at the tip of the superficial part of a broad disappearing mesenchymatic rostrum. In *Torpedo* a broad mesenchymatic rostrum is developed in early stages, but is later transformed into ligament, forming the medial part of the big ligament that extends from the antorbital cartilage frontad along the side of the head.

6. In *Raja* a "rostral appendix" develops in the frontal process of the eyebrow area. It joins the rostrum. In *Torpedo* the "rostral appendix" forms the large lateral "rostrum". In *Urolophus* no rostral appendix seems to be present.

7. In *Torpedo* the "antorbital cartilage" ("Schädelflossenknorpel") becomes very strongly developed, finlike with special articulations with the frontal part of the nasal capsule and the preorbital process. In *Raja* and *Urolophus* there is but a simple articulation with the nasal capsule, and the cartilage is not finlike but helps to support the pectoral fin.

8. The lateral process of the trabecula in *Raja* develops into a membranous (never chondrifying) subocular shelf, into which the obliquus inferior muscle of the eye is inserted. In *Urolophus* and *Torpedo* no corresponding shelf is present, the obliquus muscle being inserted into the lateral process or (later) into the lower portion of the anterior sideplate.

9. A supraorbital crest is present ontogenetically in all three rays, but in *Raja* and *Torpedo* it ends caudally with a thickening, viz. the postorbital process. In *Urolophus* this process develops separately.

10. In *Urolophus* the posterior part of the supraorbital crest develops into a large flat lamelliform process, which later fuses with the postorbital process. No such process is found in the other rays.

11. *Torpedo* has one carotid foramen, *Raja* has two foramina lying close together. In *Urolophus* the two foramina are widely separated.

12. In *Raja* an epiphysial bridge is present, in *Torpedo* and *Urolophus* no such bridge has been found (but probably will be found, as the bridge is present in adult *Narke* and in adult *Dasybatus* (*Trygon*), in the latter as two separate cartilages).

The conclusion drawn from this comparison seems to be that many of those characters in which the three genera of rays differ are more or less gradual in relation to each other.

COMMON BATHOID CHARACTERS.

The three genera agree in the following differentiated embryonic characters:

1. The broad, frontally pointed parachordal plate.

2. The joining of the polar cartilage with the basal plate by means of the acrochordal tissue and the pila antotica.

3. The fusion of the parachordals only below the notochord.

4. The long preparachordal portion of the notochord.

5. The almost total degeneration of the cranial portion of the notochord, which is raised above the parachordal plate.

6. The long preotic portion of the lamina basiotica.

7. The early closing of the hypophysial fenestra.

8. The broad trabecular plate, followed frontally by the broadened deep portion of the medial area. The skull closes dorsally (at least) by means of a tectum occipitale and a tectum synoticum (and orbitale).

9. The position of the rudiment of the cranio-quadrate process far behind the anterior end of the trabecula.

10. The presence of a supraorbital crest joined to the auditory capsule, at least during development.

11. The absence of an ectethmoid process.

12. The development of the chondrifying antorbital cartilage from the lower eyebrow area and its connections with the rostrum in front of the nasal capsule.

13. The fusion of the pharyngohyal with the auditory capsule.

14. The absence of a separate cartilage of KÄLLBERG.

15. The similar differentiation of an occipital articulation.

16. The presence of the eye stalk.

17. The early arising prefacial commissure.

18. The absence of labial cartilages. (In *Discobatcs, Narke* and others labial cartilages, however, are present.)

19. The absence of a "Basalecke".

20. No subnasal fenestra (ectethmoid chamber).

From the fact that those characters which distinguish the three families of bathoids are more or less gradual and from the preceding list of common characters it appears to follow that these bathoid groups considering the development of the neural skull, form a single unit, probably of genetical importance. The close agreement of the organization decidedly argues against the hypothesis of a polyphyletic origin of the rays, as has been suggested by certain writers. This agreement decidedly favours the idea of common bathoid ancestors.

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CHARACTERS COMMON TO SHARKS AND RAYS.

By making a comparison between those characters which are common to the sharks and those that are common to the rays it seems possible to arrive at an estimate of the possible genetical relations between these two groups.

The general outline of the early development of the skull is common to both groups. This fact seems to afford sufficient support for the generally accepted view that there is a certain genetical relation between them.

Characters common to the shark and ray embryos investigated in this paper, are:

1. Parachordals frontally pointed.
2. The polar cartilages joined with the parachordals by means of the acrochordal tissue and the pila antotica.
3. The dorsal closing of the braincase by the different tecta.
4. The presence of a prefrontal fontanella.
5. The presence of a supraorbital crest, connected with the auditory capsule at least during development.
6. The presence of an eye stalk or rudiment thereof.
7. The presence of prespiracular cartilages.

These characters, however, all belong to a group which ought perhaps to be considered to belong to the general type of selachian development. The small number of these characters undoubtedly argues against a close relationship between sharks and rays, a conclusion which will be very much strengthened by an enumeration of the embryonic characters that separate the two selachian groups.

COMMON BATHOID CHARACTERS COMPARED WITH SHARK CHARACTERS.

1. Parachordal plate broad in rays, narrow or broad (*Scyllium*) in sharks.
2. Parachordals (except in the occipital arch) fused only below the notochord in rays, surrounding it in sharks.
3. The total degeneration of the cranial portion of the notochord (except in the occipital arch) in rays, the persistence of it in the basal plate in sharks.
4. The long preparachordal portion of the notochord in rays, much shorter in sharks.
5. The long preotic portion of the lamina basiotica in rays, the short in sharks.
6. The early closing of the polar fenestra in rays, the early or late (*Scyllium*) closing of this fenestra in sharks.

7. The broad trabecular plate in rays, which is narrower in sharks (except for the later stages in *Scyllium*).

8. The position of the lateral process of the trabecula behind the frontal end of the trabecula in rays and squaloid sharks, but not in *Scyllium*.

9. The absence of an ectethmoid process in rays, but not in sharks (in *Scyllium* the process is rudimentary).

10. The cartilaginous antorbital cartilage in rays, membranous in sharks (except *Notidanids* and *Chlamydoselachus*).

11. The nasal capsule as the only component of the lamina orbitonasalis in rays (except in *Torpedo*), but not in sharks (except *Scyllium?*).

12. The fusion of the pharyngohyal with the auditory capsule in rays, with the epihyal in sharks.

13. The absence of an independent cartilage of KÄLLBERG in rays, its presence in sharks (except perhaps in *Scyllium*).

14. Condylar articulation of the skull in rays, but not in sharks (exept in *Rhina*).

15. Absence of a typical "Basalecke" in rays, its presence in notidanid and squaloid sharks.

16. Absence of palatobasal processes in rays, their presence in sharks.

17. No subnasal fenestra in rays, present in sharks (except galeoids: *Scyllium*).

18. Anterior sideplate behind the foramen of the anterior cerebral vein in rays, in front of it in sharks. In *Urolophus* both conditions are present simultaneously.

The great number of mostly important differences between rays and sharks in comparison with the small number of agreements (of less importance) decidedly point to the conclusion that the common ancestors, indicated by the general type of early development, must have belonged to a very remote period of elasmobranch development. The disagreement is really so great that one seems bound to assume a diphyletic origin of sharks and rays, (for instance from two already strongly differentiated groups of arthrodires or allied, yet still unknown, groups of Elasmobranchii).

It is obvious from the preceding list that in a number of characters *Scyllium* agrees more with the rays than with the squaloid sharks, viz. in numbers 1, 7, 9, 11?, 13?, 16 and 17. It still seems impossible to decide whether these points of agreement are due to genetical relations or are merely convergences. But the small number of these characters as compared with the great number of divergences seems rather to support the latter idea.

The result of the foregoing comparisons seems to be that, in regard to the ontogenetical development of the neural skull, *Squalus* and *Etmopterus* belong to one elasmobranch stem, *Scyllium* to another, and the bathoids to a third, the two first being more closely related to one another than to the third.

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EXPLANATION OF LETTERINGS.

a.aud.c. anterior auditory cartilage.
a.bc.c. anterior basicapsular commissure.
a.c. annular cartilage.
A.c. auditory vesicle.
a.caps. auditory capsule.
Ac.c. auditory cartilage.
Ac.pl. acustic placode.
acr. acrochordal tissue.
acr. 1. acrochordal wing.
acr. 2. saddleshaped part of the acrochordal tissue.
a.c.v. anterior cerebral vein.
a.l.c. anterior labial cartilage.
a.m.caps anteromesial wall of the nasal capsule.
ant.c. antorbital cartilage.
a.o.c. antotic cartilage.
a.v.c. antotic cartilage.
a.pr. antorbital process.
a.p.s.b. afferent pseudobranchial artery.
a.s.p. anterior side plate.
a.u.l. anterior upper labial cartilage.
b.br. basibranchial.
Be "Basalecke".
b.hy basihyal.
Br. 1 1:st branchial opening or furrow.
bt.p. basitrabecular process.
b.v. foramen for blood vessel.
c.ant. antotic cartilage.
car.e. carotis externa.
car.i. carotis interna.
carot. carotis foramen.
c.br. ceratobranchial.
ch.b. chondrified band.
ch.r. ceratohyal rays.
c.hy. (*ch*) ceratohyal.
ch.v. chierrugis vesicle.
ci.a. circumocular area.
c.K. cartilage of Källberg.
c.K.l dorsal lamella of Källbergs cartilage.
c.K.r rod of Källbergs cartilage.
c.n. cartilage nodule.
C.p. central plate.
c.p. copular plate.
c.r. cartilaginous rod
cr.pq. cranioquadrate connection.
d.c.a. dorsocaudal area.
d.end. ductus endolymphaticus.
e.a.p. anterior process of the eyebrow area.
e.br. extrabranchial.

c.c.m ecto-mesoderm.
cct. ectethmoid process.
c.f. "empty" foramen.
c.f.a. extra fascial area.
c.m. eye brow mesenchyma.
ent. entodermal gut.
c.pa epiphysial area.
Ep.br. ep.br. epiphysial bridge.
ep.hy epihyal.
ep.pr. epiphysial process.
c.pq. extrapalatoquadrate blastema.
c.pq.a. extrapalatoquadrate area.
c.st. eye stalk.
ct.can ethmoid canal.
f.a. frontal area.
f.bc. fenestra basicapsularis.
f.cnd. foramen endolymphaticum.
f.f. frontal field.
f.hm. foramen nervi-hyomandibularis VII.
f.pit. pituitary fossa.
f.pro. foramen prooticum.
f.psb pseudobranchal foramen.
fr.a. frontal area.
fr.w. frontal wall
f.vest. fenestra vestibuli.
g.f. glandular field.
hm hyomandibular.
hm VII foramen for N. hyomandibularis VII.
hyp. hypophysial fenestra.
hyp.loc. location of the hypophysis.
hy.r.b. basal part of hyal rays.
i.arc. (*I, II* . . .) interarcual (I, II . . .).
i.n.a. internasal area.
i.n.f. internasal field.
i.n.s. internasal septum.
i. o.f. infraorbital field.
i.o.l. infraorbital line.
j.v. jugular vein.
k.pr. keel-process of the basis cranii.
lab.c. labial cartilage.
l.bas. 1. lamina basiotica anterior.
l.bas. 2. lamina basiotica posterior.
l.bd. ligamentous band
l.bo. lamina basiotica.
l.c. lateral commissure.
l.c.r. lateral commissure ray.
l.e.a. lower eyebrow area.
l.f.c. labial flap cartilage = medial raphe.
lig. ligament.
l.c. lower labial cartilage.
l.mes. lateral mesenchymatic mass of the trabecula.
l.n.caps. lateral nasal cartilage.
l.o.n. lamina orbito-nasalis.
l.rost. lateral rostral lamella.
l.r.r. lateral rostral rod.
m.a. medial area.
m.cor.hm. musculus coraco-hyomandibularis.
md.a. mandibular arch.
m.depr.r. musculus depressor rostri.
m.lev.lab. musculus levator labii.
m.n.caps. medial wall of the nasal capsule.
m.o.i. musculus obliquus inferior.
m.o.s. musculus obliquus superior.
M.p. marginal plate.
m.r.e. musculus rectus externus.
m.r.s. musculus rectus superior.
m.Sc. sclerotic lamella of the 1:st somite.
m.S.1. medial lamella of the 1:st somite.
m.s.l. mandibular sensory line.
my. myolome.
n.a. nasal aperture.
n.ar. nasal area.
n.bucc. VII. nervus buccalis VII.
n.caps. nasal capsule.
n.caps.l. lateral rudiment of the nasal capsule.
n.caps.m. medial rudiment of the nasal capsule.
n.ch. notochord.
n.ch.gr. notochordal growe.
n.cr. (*1, 2, 3, 4*) 1:t—4:th portion of the neural crest.
n.cr.m. neural crest material.
n.et. nervus ethmoidalis.
N.f. nasal fenestra.
n.f.c. nasal flap cartilage.
n.opht.V. nervus ophthalmicus V.
N.p. neuroporus.
n.pal. nervus palatinus.
n.pl. nasal placode.
n.prof. nervus ophthalmicus profundus.
n.s. nasal sac.
n.th. nervus thalamicus.
Nu.p. Nuchal plate.
o.a. oral arch.
o.a.br. branch of the orbital artery (foramen).

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o.br. outline of the brain.
o.c. occipital column.
o.cc., occ.n. occipital nerve.
o.f. occipital field.
o.n.v. orbitonasal vein.
op.V. n. ophthalmicus superficiales V.
op.VII. n. ophthalmicus superficiales VII.
Op.V.pl. ophthalmicus V placode.
Op.VII.ggl. opthalmicus VII ganglion.
o.pr. orbital process.
opt.f. optic fenestra.
opt.v. optic vesicle.
orb.a. orbital artery.
orb.a.b. branch of orbital artery.
orb.c. orbital cartilage.
or.s.l. oral sensory line.
o.sin. orbital sinus.
o.s.l. otical sensory line.
p.a. parietal area.
pal.n. palatine nerve.
p.ant. pila antotica.
par.f. parietal field.
p.aud.c. posterior auditory cartilage.
p.b. polar cartilage.
p.bc.c. posterior basicapsular commissure.
p.c. parachordal.
p.ch.r. prochondrial rod ("supraspiracular" cartilage).
p.c.v. posterior cerebral vein.
pect.f. pectoral fin.
ped. pedicle.
p.f.c. prefacial commissure.
p.f., p.fen. polar fenestra.
ph.br. pharyngobranchial.
ph.hy. pharyngohyal.
Pi.p. pineal plate.
pit.c. pituitary commissure.
pit.v. foramen for the pituitary vein.
p.l.c. posterior labial cartilage.
p.lig. basitrabecular ligament.
p.l.r. preopercular sensory line rudiment.
P.m.p. postmarginal plate.
P.mx.p.? premaxilar plate.
P.nu.p. paranuchal plate.
p.n.a. prenasal area.
P.n.p. postnasal plate.
p.o.a. preoral area.
p.occ. pila occipitalis.
po.na. postnasal area.
P.o.p. preorbital plate.
p.orb.a. postorbital area.
p.orb.c. preorbital canal.
p.orb.cr. preorbital crest.
P.orb.p. postorbital plate.
po.sp.bl. postspiracular blastema.
p.p. pila prootica.
p.p.c. postpituitary commissure.
p.pr. palatine process.
pq. palatoquadrate.
pq.p. palatine part of the palatoquadrate.
pq.tr. quadrato-trabecular membrane.
pr.IV. primitive trochlear nerve.
pr.ant. antorbital process.
pr.c. precarotid commissure (for inst. in fig. 98).
pr.c. preorbital cartilage (for inst. in fig. 114).
pr. can. preorbital canal.
pr.d. processus dorsalis.
pr.m. premandibular mass. (Dohrn).
pr.neur. processus neuroporicus.
prof. profundus nerve.
prof.ggl. profundus ganglion.
prof.pl. profundus placode.
proot.f. prootic foramen.
pr.ot.l. preotic lamina.
pr.p. preorbital process.
pr.po. postorbital process.
p.r.r. pretrabecular rod.
pr.sp.a. prespiracular area.
p.s.b. efferent pseudobranchial artery.
p.s.c. posterior semicircular canal.
ps.hy. pseudohyal.
p.s.l. postorbital sensory line.
P.s.op. postsuborbital plate.
p.s.p. "posterior side plate".
p.sp.a. prespiracular area.
p.u.l. posterior upper labial cartilage.
R. rostrum.
r.c. rodlike cartilage of the otical shelf.
r.g.p. rudimentary gill-pouch of van Bemmelen.
r.lig. rostral ligament.
rostr.ap. rostral appendix.
rostr.r. rostral rudiment.
r.pl. rostral plate.
S.1—S.4 Somite 1—4.
S.1.a = anterior process of the 1:st Somite = Platts vesicle.
S.1.com. premandibular commissure.

S.1.p. posterior process of the 1:st Somite.
S.2.m.—*S.3.m.* Muscular process of the 2d and 3d somite.
S.2.m.pr.—*S.4m.pr.* Muscular process of the 2d to 4th somite.
s.c.a. sclerotic area.
s.cr. supraorbital crest.
S.e. superior eyebrow.
s.e.f. subectodermal field.
scns.c. sensory line cartilage.
s.l.o.a. sensory line of the oral arch.
Sn.f. subnasal fenestra.
s.o.a. supraorbital area.
s.o.c.c. subocular cartilage.
s.o.c.s. subocular shelf.
s.o.f. supraorbital field.
s.o.l. supraorbital sensory line.
S.o.p. suborbital plate.
s.o.s. subotical shelf.
sp.c. "Spangenknorpel".
Spir. = spiracle.
spir.c. prespiracular cartilage.
spir.l. lateral spiracular rudiment.
spir.o. = spiracular sensory organ.
spir.p. posterior spiracular rudiment.
s.r.r. suprarostral rod.
sy.c. symphysial cartilage.
symp. symplecticum.
tae.a. taenia marginalis area.
taen. taenia marginalis.
taen.med. taenia medialis.
t.b. teeth blastema + palatine process.
t.b.$_2$ teeth blastema.
t.occ. tectum occipitale.
t.orb. tectum orbitale.
t.pl. tooth plate.
trab. trabecula.
trab.a. trabecular area.
trab.p. lateral trabecular process.
trab.q.c. and *tr.pq.* trabeculo-quadrate connecting lamella.
t.syn. tectum synoticum.
u.e.a. upper eyebrow area.
u.r.md. = unpaired rudiment of the mandibula.
v.f. foramen for vein.
v.jug. vena jugularis.
v.P. vesicle of Platt.
x. thickening of the epidermis.
y. occipital nerve y foramen.
II. optic foramen.
III. oculomotor foramen.
III.V.c. oculomotor-trigeminus commissure.
IV. trochlear nerve or foramen.
V. trigeminal nerve or foramen.
V.c. trigeminal epibranchial contact.
V.ep.pl. trigeminal epibranchial placode.
V.lat. lateralis placode of trigeminal.
V.pl. trigeminal epibranchial placode.
V.pl.n. trigeminal lateralis placode nerve.
VI. abducens nerve or foramen.
VII. facialis nerve or foramen.
VII.c. facialis epibranchial contact or placode.
VII.ggl. facialis ganglion.
VII.lat. lateralis placode of facial nerve.
VII.lat. lateralis VII fibres (foramen for).
VII.lat.org. sensory organ of lateralis VII placode (epibranchial).
VII.pl. flacialis nerve (placode of).
VIII. acustic nerve or foramen.
IX. glossopharyngeal nerve or foramen.
IX.lat.ord. sensory organ of IX.
IX.pl. glossopharyngeal epibranchial placode.
X. vagus nerve or foramen.
X.br. vagus branche, (foramen for).
X.lat.org. sensory organ of X.

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